

A MONOGRAPHIC REVISION OF THE ANT GENUS *PONERA* LATREILLE (Hymenoptera: Formicidae)^{1,2}

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Abstract: Most species of *Ponera* (s. lat.) may be assigned to a newly delimited genus taking the name *Hypoponera* Santschi (new status, for *Ponera* subgenus *Hypoponera*). The 28 living and 1 extinct species remaining in *Ponera* are monographed, following discussion of the new generic classification. Species described as new are: *Ponera alpha*, *P. augusta* (NE New Guinea); *P. borneensis* (Borneo); *P. chapmani* (Negros, Philippines); *P. manni* (Viti Levu, Fiji), *P. loi* and *P. woodwardi* (Upolu, Samoa).

This is the first of a series of proposed papers dealing with those species assigned to the ant genus *Ponera* in the classification of Emery (1911) and Wheeler (1922). The Emery-Wheeler system has been subject to considerable recent change and will no longer operate successfully in the light of modern knowledge. Recent research has necessitated synonymy of many older genera, as they have merged one into another on critical examination of their status.

This paper offers yet another generic change, in this case not a synonymy but a split; for it demonstrates that *Ponera* (*sensu lato*) consists of two distinct, non-cognate, and easily distinguished genera. True *Ponera* contains only 28 living species confined to the Indo-Australian area, eastern North America and Europe; while the second genus receives most of the former *Ponera* species, including all of the Neotropical and Ethiopian forms.

This last assemblage takes the name *Hypoponera* Santschi (1938) which was originally assigned subgeneric status under *Ponera*. Santschi's morphological criteria of *Hypoponera* are taxonomically meaningless, but his type species, *Ponera abeillei* André 1881, belongs in my second genus which must be named accordingly.

In addition this study provides a world revision of *Ponera*, in the newly restricted sense. I have examined many hundreds of specimens of *Ponera* (*sensu lato*), including most types. Consequently it can be confidently claimed that all species previously described in *Ponera*, and congeneric with the type, *P. coarctata*, are included here. As a sideline to the main study Heer's form-genus *Poneropsis* has been utilized as a parataxonomic category, containing all but one of the many fossil ants previously assigned to *Ponera* (Taylor 1964).

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REFERENCE COLLECTIONS

Proper systematic study of ants is usually impossible without access to type material. This is especially true when considering large, long-standing genera like *Ponera*. In this regard I have obtained splendid cooperation from the curators of many museums and other institutions, and have been able to study almost all required type specimens. At present all types in *Ponera* (*sensu lato*) have not been examined, since the primary task of establishing the new generic limits has been possible without this. However, I have seen types, or dependably type-compared specimens, of all erstwhile *Ponera* species from areas where the genus in its present sense occurs, as well as those of most African and South American species properly assigned to *Hypoponera*. In revising *Ponera* it has thus been possible to proceed with several revisionary studies of *Hypoponera*. In the systematic treatment of *Ponera* species to follow, each loan of reference material is noted. Notice is not given to all loans made for the major study of which this paper is a part since many consignments contained only *Hypoponera* species. However, in the list of cooperating institutions given below, all those that have assisted with the project are included, and the persons involved are acknowledged in the relevant section following.

The principal collections from which types or details concerning them have been obtained are the following (abbreviations in brackets are those used in the text): American Museum of Natural History, New York City (AMNH); British Museum (Natural History), London (BMNH); Clark Collection, National Museum of Victoria, Melbourne, Australia (Clark Coll.); National Insect Collection, Commonwealth Scientific and Industrial Research Organization, Canberra, Australia (CSIRO); Emery Collection, Museo Civico di Storia Naturale, Genoa, Italy (Emery Coll.); Forel Collection, Musée d'Histoire Naturelle, Geneva, Switzerland (Forel Coll.); Hungarian National Museum, Budapest (Hung. N. M.); Mayr Collection, Naturhistorisches Museum, Vienna, Austria (Mayr Coll.); Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ); Oxford University Museum, Oxford, England (Oxford Coll.); Paris Museum, Paris, France (Paris Mus.); Santschi Collection, Musée d'Histoire Naturelle, Basel, Switzerland (Santschi Coll.); United States National Museum, Washington, D. C. (USNM).

Valuable general collections have been received from the following institutions: AMNH; B. P. Bishop Museum, Honolulu, Hawaii (BISHOP); Canada Department of Agriculture, Entomological Research Branch, Ottawa (CDA); Cornell University, Department of Entomology, Ithaca, New York (Cornell Coll.); CSIRO; Secretaria da Agricultura, São Paulo, Brazil (Sec. Ag. Brazil); University of Queensland, Department of Entomology, Brisbane, Australia (Queensland U. Coll.). Several private collections, including those of Fathers Borgmeier and Kempf, Father Lowery, Dr Collingwood and Profs. Weber and Yasumatsu were of great value.

The primary source of material has been the Museum of Comparative Zoology at Harvard University. Among its included collections of special interest here are those of W. M. Wheeler, W. M. Mann, E. O. Wilson and W. L. Brown, together with the Philippine collections of James W. Chapman, the B. Finzi European collection and most of the South-west Pacific, New Guinean and Australian material collected by me in 1962.

The MCZ has been the primary place of deposition for my holotypes and other reference material. The following collections contain representative specimens, including paratypes

as detailed below under the relevant species headings: AMNH, BISHOP, Borgmeier-Kempf Coll., BMNH, CSIRO, Emery Coll., Forel Coll., Yasumatsu Coll. Less representative collections have been placed in many of the contributing institutions listed above.

FIELD STUDIES

During the period 1959–1963, field work directed mainly towards these studies was carried out in the United States, in Central America (Barro Colorado I., Panama Canal Zone, and Republic of Panama), and various parts of the SW Pacific, New Guinea and Australia. The latter areas were most significant for material of *Ponera* (*sensu stricto*). The Australasian field studies occupied seven months (10 February–10 September 1962). Eighteen days (13 February–2 March) were spent on Viti Levu, Fiji Is., and 25 days (3–28 March) on Upolu, Savaii and Tutuila in the Samoan Group. The remaining time was spent in eastern Australia, except for a period in NE New Guinea and Papua (1–30 August). These studies were supported primarily by the Committee on Evolutionary Biology of the Department of Biology at Harvard and by a traveling fellowship from Harvard University. The New Guinea and Samoan studies were financed by an award from the Bache Fund Committee of the American Academy of Arts and Sciences, and a Grant-in-Aid of research from Sigma Xi-RESA.

Discussion of the major collecting localities in Australia, New Guinea and Fiji will be presented elsewhere, and details of the Samoan field studies are given in a forthcoming monograph on the ants of Polynesia (Wilson & Taylor, 1967, Pac. Ins. Mon.).

Ponera specimens were taken at only one Fijian locality, Nandarivatu, in the north-central part of Viti Levu. Nearly all Samoan species were taken widely on Upolu and Savaii, but the most significant locality was Afiamalu in the center of Upolu. Many *Hypoponera* specimens were collected in Australia, but *Ponera* was taken only occasionally. In New Guinea, specimens were obtained at most localities, but the most valuable collections are from the Bulolo River valley near Wau; or the rain forest preserve of the Highlands Agricultural Station at Aiyura. The principal factor determining importance of the various collections was whether it was possible to operate Berlese funnels at the localities involved. The significant collecting areas are, in fact, those where prolonged operation of funnels, using electrical heating was possible. The usefulness of the Berlese funnel cannot be over-emphasized; tremendous increase in the number of known cryptobiotic ants will doubtless take place as its use becomes more widely practicable.

Acknowledgments: The field studies depended on the generous cooperation of many people. The Fijian studies were possible through cooperation of J. R. Angus, Conservator of Forests, and members of his staff, D. K. Paul, R. S. Wyatt and C. G. S. Johns. Special thanks are due B. E. V. Parham and G. Ettershank (Western Samoan Department of Agriculture), G. J. Keys (Apia Observatory), W. Lidgard (Vaipouli, Upolu) and Chief Va'ai (Lotogo, Savaii). In Australia thanks are due to members of the Entomology Department, University of Queensland, especially Dr T. E. Woodward, F. Perkins and Miss E. Exley. K. C. S. Harley (CSIRO, Ingham), G. Saunders and P. Twomey (Queensland Department of Agriculture, Atherton) gave invaluable assistance in N. Queensland. In Sydney Dr J. W. Evans and C. N. Smithers (Australian Museum) were most helpful, as was Father B. B. Lowery. At Canberra the assistance of Dr D. F. Waterhouse, Dr K. H. L. Key, E. F. Riek and T. Greaves (CSIRO) is gratefully acknowledged. Like many biologists who have

visited New Guinea I owe much to Dr J. J. H. Szent-Ivany, entomologist to the Department of Agriculture at Port Moresby, and to his wife. Dr J. L. Gressitt (Bishop Mus.) allowed use of his Museum's field station and vehicle at Wau, where Mrs J. Sedlacek was of great assistance. J. A. Barrett, entomologist at Aiyura, was most helpful in many ways.

The following persons are gratefully acknowledged for providing specimens and information concerning them: Dr G. Ayre, Belleville, Canada (CDA); the late Dr Erzébet Bajáry (Hung. N. M.); Dr C. Besuchet (Forel Coll.); A. N. Burns (Clark Coll.); Prof. W. G. Carter, University of Oklahoma; the late Dr J. W. Chapman, San Mateo, California; Dr C. A. Collingwood, Reading, England; Dr M. Fischer (Mayr Coll.); the late Dr H. J. Grant, Philadelphia Academy of Sciences; Dr P. J. M. Greenslade, Guadalcanal, British Solomon Islands; Dr J. L. Gressitt (BISHOP); Dott. Delfa Guiglia (Emery Coll.); Dr K. Hayashida, Hokkaido University, Japan; Dr G. P. Holland, Ottawa, Canada (CDA); Prof. P. B. Kanno, University of North Dakota; Dr F. Keiser (Santschi Coll.); Father W. W. Kempf, São Paulo, Brazil (Borgmeier-Kempf Coll.); Mme Simone Kellner-Pillault (Paris Mus.); G. E. J. Nixon (BMNH); Dr A. Raignier, Louvain, Belgium; Dr E. S. Ross, California Academy of Sciences (CAS); Dr J. G. Rozen (AMNH); Dr M. R. Smith (USNM); Dr Mary Talbot, St Charles, Missouri; Dr E. Taylor (Oxford Coll.); Prof. J. K. A. Van Boven, Louvain, Belgium; Prof. N. A. Weber, Swarthmore College, Pennsylvania; Prof. G. C. Wheeler, University of North Dakota; Prof. K. Yasumatsu, Kyushu University, Japan.

Professor Edward O. Wilson and other members of Harvard University, notably Professors F. M. Carpenter, P. J. Darlington, and E. Mayr, have given freely of their time and advice. I am also greatly indebted to Dr W. L. Brown, Jr., of Cornell University.

GENERIC PARTITION OF *PONERA* (*Sensu lato*)

As noted previously, "*Ponera*" of the Emery-Wheeler classification is divided here into two genera, taking the names *Ponera* Latreille, and *Hypoponera* Santschi.

In the "Genera Insectorum" (Fasc. 118, 1911) Emery listed 50 species under "*Ponera*" with 25 subspecies and varieties (not including synonyms). Only five of these (*clavicornis*, *coarctata*, *japonica*, *pennsylvanica* and *selenophora*) are included here in *Ponera* (*s. str.*); the remainder almost all belong in *Hypoponera*. Two further *Ponera* (*s. str.*) species were listed by Emery in genus *Cryptopone* (*mocsaryi* Szabo [now replaced as a homonym by *szaboi* Wilson] and *tenuis* [Emery]). However, relationship between some true *Ponera* species was noted, prior to 1911, by both Emery and Wheeler. Following Emery (1895) both considered *pennsylvanica* a subspecies of *coarctata*, and both observed the affinity between *japonica* and *coarctata* (Wheeler 1906a; Emery 1909). Emery (1900) noted relationship between his new species, *selenophora* and *clavicornis*, but at the same time he described *tenuis* in *Cryptopone*. Forel, on the other hand, had managed to describe two *Hypoponera* species as subspecies of *Ponera coarctata* prior to 1911!

In 1933 Wheeler almost realized the generic split along the lines I am proposing. He recognized the affinity of eight Indo-Australian species and segregated them in two closely related new genera, *Pseudocryptopone* and *Selenopone*. All of these are members of *Ponera*, as delimited here, except *zwaluwenburgi* Wheeler, which is one of the most convergently *Ponera*-like of all *Hypoponera* species. Wheeler considered *Pseudocryptopone* and *Selenopone* close to "*Ponera*" and admitted his inability to circumscribe *Pseudocryptopone* in stating

that "one of the species, *incerta*, which I have assigned to *Pseudocryptopone*, might, with equal propriety, be placed in *Ponera*." His separation of *Selenopone* was also stated to be "tentative." He evidently considered that the partitioning of these "genera", even without clearly stating their limits, was a worthwhile step towards the subdivision of an already unwieldy "*Ponera*"—"a large and difficult genus in great need of careful revision." The specific composition of his genera indicated that Wheeler appreciated the affinity of some species now included in *Ponera* (*s. str.*), but his concept was almost entirely intuitive as indicated by his vague generic limits. He also failed to include in *Selenopone* and *Pseudocryptopone* other Indo-Australian species of true *Ponera*, several of which he himself had described. Moreover, he completely overlooked the fact that the *Pseudocryptopone* and *Selenopone* species were congeneric with each other and with *P. coarctata*, the type species of *Ponera*. As with most earlier authors, "typical *Ponera*" to Wheeler included those species now assigned to *Hypoponera*, and the true *Ponera* species of the Indo-Australian area were to him a vaguely delimited group of rare, peculiar forms. This is evident in his statement that "the species closely related to *tenuis*, after all, have a habitus distinctly different from the typical species of *Ponera*."

In 1957 Wilson synonymized *Pseudocryptopone* and *Selenopone* under *Ponera* (*s. lat.*), and erected two "species groups" (those of *tenuis* and *selenophora*) to contain them. Wheeler's previously overlooked species, *scabra* and *sinensis*, were added to the series along with several new species. The *tenuis* and *selenophora* groups thus included all previously described Indo-Australian species now placed in *Ponera*, except *taipingensis*, *japonica*, *leae*, and its subspecies *norfolkensis*. However, *zwaluwenburgi* was still included, and the relationship between the other species and *coarctata* again went unrealized. Once more the species now placed in *Hypoponera* were considered to be "typical *Ponera*." Addition of *leae* and *norfolkensis* to Wilson's *tenuis* group was made by Taylor (1960), and M. R. Smith (1962) added a new species, *P. exotica*.

The major conceptual advance reported here is the realization that the species discussed by Wheeler and Wilson form a single generic group, congeneric with *P. coarctata*. The positions of *taipingensis*, *japonica*, *leae*, *norfolkensis*, *pennsylvanica* and *zwaluwenburgi* are clarified, and a number of new species are described.

Ponera and *Hypoponera* share many characters. Similar morphoclineal sequences are evidenced, probably indicating parallelism in their evolutionary histories. However, when one examines segmentation of the oral palpi, structure of the subpetiolar process of the workers and females, the male genital characteristics, and distribution and numbers of certain specialized larval tubercles, it is obvious that two separate lineages are represented. A number of more general characters such as details of mandibular, mesosomal and node form, are combined in all *Ponera* species, providing the genus with a strikingly uniform and characteristic habitus. Although these structures may be separately developed in some *Hypoponera* species, close general resemblance to *Ponera* is only rarely attained.

The newly defined generic groups may be characterized as follows:

Genus *Ponera* Latreille

Ponera Latreille, 1804, Nouv. Dict. Hist. Nat. **24**: 178-179. Type species—see discussion below.

Pseudocryptopone Wheeler, 1933, Amer. Mus. Nov. **672**: 12–13. Type species: *Cryptopone tenuis* Emery, orig. desig. Synonymy by Wilson, 1957.

Selenopone Wheeler, 1933, Amer. Mus. Nov. **672**: 19. Type species: *Ponera selenophora* Emery, orig. desig. Synonymy by Wilson, 1957.

TYPE SPECIES AND NOMENCLATURE. There is a problem regarding these subjects; two type species have been previously designated for *Ponera* and conventional usage has recognized the junior one of these since 1840.

The name *Ponera* was assigned by Latreille (1804) to a group of species [including *Formica coarctata* Latreille 1802a (= *Formica contracta* 1802b) and *Formica crassinoda* Latreille 1802b] which he had previously named “famille des fourmis étranglées” (1802a: 65) or “les FOURMIS ÉTRANGLÉES *Form. coarctatæ*” (1802b: 195). At the time of its inception no type species was formally designated for the genus, but Latreille later (1810: 437) cited *Formica crassinoda* as the type. This citation is valid under Opinion II of the International Commission on Zoological Nomenclature and its qualifying Opinion 136 which discussed the interpretation of Latreille's 1810 work.

A second type species for *Ponera*—*Formica contracta* Latreille (1802b) (a junior objective synonym of *Formica coarctata* Latreille (1802a))—was proposed by Westwood (1840).

In 1858 Fredrick Smith erected the genus *Pachycondyla* for the species previously included in *Ponera*, but congeneric with *Formica crassinoda* Latreille, 1802. No type species was designated, but Emery formally cited *crassinoda* as the type of this genus in 1901 (Emery 1901).

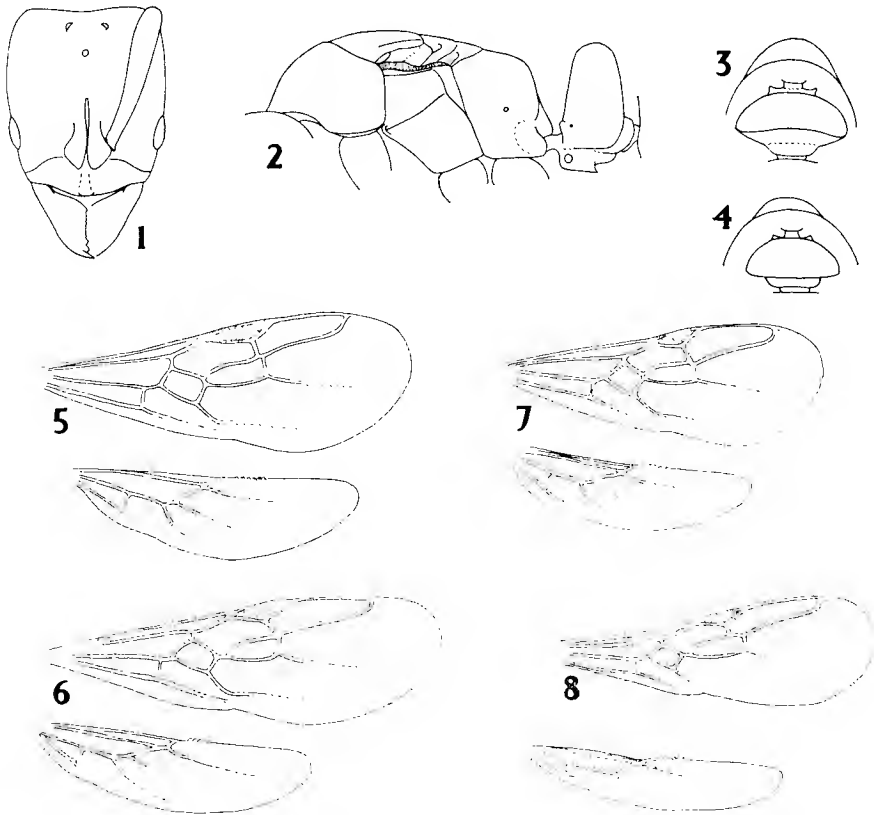
The names *Ponera* Latreille 1804 (*sensu* Westwood 1840), and *Pachycondyla* Fr. Smith, 1858 (*sensu* Emery 1901) have been universally and consistently used since their original proposal.

This situation was discussed by Benson, Ferrière and Richards (1947), who urged the International Commission to set aside Latreille's designation of *Formica crassinoda* as the type species of *Ponera*, thus maintaining nomenclatural stability. In 1950 (Bull. Zool. Nomencl. **4**(13/15): 351–446) the Commission ruled to postpone consideration of the case until additional information was obtained. In view of the strong case for the procedures requested by Benson, Ferrière, and Richards, I have accepted current usage, rather than strict priority, in applying the name *Ponera*. It is thus being used here in the sense of Westwood (1840) and subsequent authors with *Ponera coarctata* (Latreille), 1802 as type species. A statement of the difficulties apprehended if the International Code were strictly applied to this case is being prepared for consideration by the Commission.

DIAGNOSIS. Important characters distinguishing *Ponera* from *Hypoponera* are *italicized*.

Worker: Small to medium size ponerine ants; head width ranging about 0.3–0.85 mm. Head longer than broad, roughly rectangular in frontal view, sometimes prismatic behind. Mandibles triangular, with 3 enlarged apical teeth followed by a series of small to minute, more or less regular denticles; several of these occasionally enlarged. No basal mandibular pit or groove. Palpal formula: *Maxillary* 2: *Labial* 2. Clypeus simple, often produced anteriorly, or with a raised tumosity or distinct tooth on the middle of its antero-dorsal face. Eyes small, with 1–15, usually very indistinct, facets; situated about 0.75–0.90× the distance from lateral occipital border to midpoint of anterior genal border. Scapes seldom exceeding median occipital border, their apices usually approximately con-

tiguous with it, or failing to reach it by up to twice their maximum thickness. Funiculus incrassate, apical segment subequal in length to the two preceding together; an indistinct to distinct 4- or 5-segmented club often present. Mesosoma elongate, sides more or less parallel, dorsal profile usually flat. Posterolateral edges of propodeum sometimes marginate, forming angles of about 70° - 90° when viewed from above. Mesometanotal and lateral mesonotal sutures may be absent. Mesepisternum not divided by a horizontal suture. Middle and posterior tibiae each with a single pectinate apical spur; middle tarsi lacking setose bristles on their outer surfaces. Petiolar node massive; relatively thick in side view, usually tapering only slightly dorsally; seen from above, its anterior face more or less semi-circular, the posterior one transverse, weakly concave to feebly convex. Dorsal and posterior faces of node forming a single arched surface, or with junction between them obtusely marginate. Edge between anterolateral, and posterodorsal faces of node rounded or marginate. *Subpetiolar process highly characteristic*: usually shallow; with a rounded

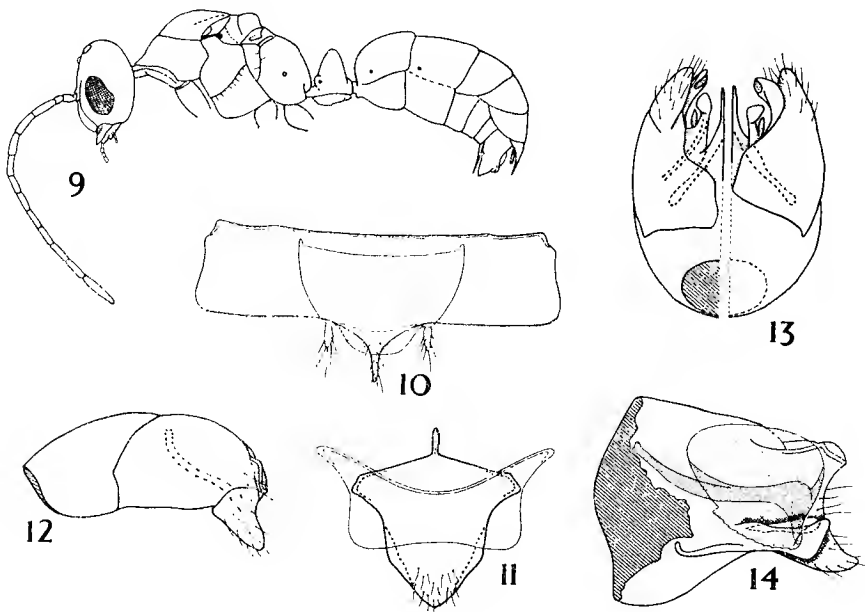


Figs. 1-8. *Ponera* ♀ characters. *P. pennsylvanica* Buckley: 1, head; 2, mesosoma and node; 3, node, dorsal view; 5, wing venation. *Ponera coarctata* (Latr.): 4, pronotum outline and node, dorsal view. Indo-Australian *Ponera*, forewing and hindwing venation: 6, *P. chapmani* n. sp., ♀ (Paratype); 7, *P. woodwardi* n. sp., ♀ (Paratype); 8, *P. swezeyi* Wheeler, ♀ (Upolu, Samoa). See text for explanation.

or bluntly angled anteroventral corner, and a more or less distinctly angular posteroventral one. *Latter composed of 2 separate, small to large, right-angled to acute teeth, situated side by side*, and sometimes inclined posterolaterally. *Anteriorly, subpetiolar process with a more or less distinct circular or oval thin-spot, or fenestra*, visible in transmitted light.

♀. General features as shown in figs. 1-2. Basically similar to worker, with the usual characters of full sexuality—well developed compound eyes, ocelli, complete mesosomal structure, and wings. Identical to conspecific workers in mandibular, palpal, clypeal, and antennal structure. Petiolar node in side view usually thinner; subpetiolar process similar, usually slightly more shallow. Wing venation as in figs. 5-8, 2 closed cubital cells, single closed discoidal and radial cells. Venation usually of "*coarctata* type" (fig. 5), with 2nd abscissa of the radial sector+median vein ($Rs+M.2$) arising proximal to anterior base of mediocubital crossvein ($m-cu$). Two unrelated species, *P. chapmani* and *P. swezeyi* (figs. 6, 8) have $Rs+M.2$ arising distally to $m-cu$. Anal lobes absent on hindwing; middle and posterior tarsal spurs as in worker.

♂. (figs. 9-14). All known specimens are winged; ergatoids are apparently not developed. Mandibles vestigial, with a single apical tooth. *Maxillary palpi 2-5-segmented, labial palpi 2-segmented*. Parapsidal furrows distinct, notauli absent. Wing venation as in conspecific ♀♀, anal lobe absent from hindwing. Cerci present; *pygidium with a strong sclerotized terminal spine* (fig. 10). *Subgenital plate broad, bluntly pointed*. Genital capsule as



Figs. 9-14. *Ponera*, ♂ characters (*P. pennsylvanica* Buckley): 9, lateral view, wings and legs removed; 10, tergites VII (pygidium) and IX+X, flattened, dorsal view; 11, sternites VIII and IX (sub-genital plate), flattened, ventral view; 12, genital capsule, lateral view; 13, genital capsule, dorsal view (right); ventral view (left); 14, genital capsule, mesal view of right 1/2, dissected to show penis valve, volsella, and inner aspect of gonoforceps.

in figs. 13-14. *Gonoforceps* with a peculiar sclerotized posterodorsal process which is usually low, with a thickened marginal ridge; or it may be narrowly digitate and inclined mesally. This structure is apparently unique to *Ponera*. Tarsal spurs as in ♀ castes.

Larva: This stage has been described and illustrated in detail for *P. pennsylvanica* by G. C. & J. Wheeler (1952: 631, pl. V, figs 18-21, 28-32). There is apparently nothing unusual in the general body shape or cephalic structure. The body bears about 150 papilliform tubercles, each surmounted by a strong spine. Such structures are present in many larval Ponerini. The exceptional character, apparently allowing generic diagnosis of *Ponera* larvae, is the presence of 3 or 4 pairs of peculiar mushroom or doorknob shaped *glutinous tubercles*, on the dorsa of abdominal segments III-V or III-VI. Their number and arrangement is characteristic of *Ponera*, although similar organs are present in other genera of tribe Ponerini (see discussion below under *Hypoconera*).

Pupae: Enclosed in cocoons in all known cases except *P. tenuis*, which lacks cocoons in all castes; this exceptional condition is very rare in ponerine ants.

Genus *Hypoconera* (Santschi) new status

Ponera subgenus *Hypoconera* Santschi, 1938, Bull. Soc. Ent. Fr. 43: 79. Type species: *Ponera abeillei* André, original designation.

HISTORICAL. *Hypoconera sensu* Santschi included those species of *Ponera* (*s. lat.*), lacking an incised mesometanotal suture on the mesosomal dorsum. This character, in fact, has no diagnostic value at the generic level. However, Santschi cited *Ponera abeillei* André as type species of *Hypoconera*; so this name is available for the present taxon. At the time of its inception, 13 African, 5 Indo-Australian, and 3 American species were listed under *Ponera* (*Hypoconera*). All of these belong in *Hypoconera*, except *clavicornis*, *japonica*, and *scabra*, which are true *Ponera* species. Santschi's concept was thus almost meaningless in terms of the present classification.

DIAGNOSIS. (Based on numerous specimens of many species including all stages and castes. Slight future modification may be necessary, but this almost certainly could not affect the status of the genus. Characters differentiating the species from those of *Ponera* are italicized.)

Worker: Cephalic structure similar to *Ponera*. Mandibles triangular, with 3 or 4 enlarged apical teeth; posterior masticatory border edentate, finely denticulate, or with distinct large teeth. No basal mandibular pit or groove. Palpal formula: *Maxillary 1: Labial 1 or 2*; maxillary palpus minute, sometimes difficult to discern. Clypeus simple, rarely with a median denticle. *Eyes sometimes lacking*, but usually as in *Ponera*. Scapes as in *Ponera*, funiculus incrassate, only occasionally with a segmentally differentiated 4- or 5-jointed club. Mesosomal structure variable, at one extreme similar to that of *Ponera*, at the other *Brachyponera*-like, with a complex dorsal profile. Mesometanotal and lateral mesometanotal sutures present or absent; mesepisternum undivided by a horizontal suture. Middle and posterior tibiae each with a single pectinate spur; middle tarsi lacking setose bristles on outer surfaces. Form of petiolar node variable, usually higher and thinner in side view than in *Ponera*. *Subpetiolar process* a simple lobe—*never with a fenestra or paired posterolateral teeth*.

♀. General features as in worker, petiolar node usually thinner in side view. Palpal formula, mandibular, clypeal, and antennal structure, tibial spurs, and form of subpetiolar

process as in worker. Compound eyes and ocelli well developed. Mesosomal structure complete; parapsidal lines distinct; notauli wanting. Wing venation as in *Ponera*, no anal lobe on hindwing.

♂. Two types are known: winged ♂♂ of normal form are present in most species, while wingless *ergatoid* ♂♂ are found in others. The latter have apparently been evolved several times; those of some species are much more worker-like than others, and they may have 12 or 13 antennal segments (see Smith & Haug 1931; Smith 1939). *Maxillary palpus with a single reduced segment*. Labial palpus with 1 to 4 segments. In the normal winged ♂♂, parapsidal furrows distinct, notauli occasionally present, wing venation as in ♀♀, anal lobe lacking on hindwing. *Pygidial spine wanting*; cerci present; *gonoforceps* simple, *lacking posterodorsal process seen in Ponera* ♂♂, basal portions often expanded, with apices narrowly digitate; subgenital plate often spatulate.

Larva: Similar to those of *Ponera*, but with 2 pairs of doorknob-shaped *glutinous tubercles* on abdominal segments IV and V. These are present in all known instars of all castes. Some species also have flap-like outgrowths on the lateroventral aspects of the 1st thoracic segment (G. C. & J. Wheeler 1952), and others have tiny doorknob-shaped tubercles on the ventral aspects of the abdomen. The pupae, with one known exception (*H. monticola* (Mann)), are enclosed in cocoons.

DISCUSSION. Immature stages are known for about 30 *Hypoponera* species, from New Guinea, Australia, Polynesia, North and Central America, Brazil, and the Ivory Coast. The larval characters are thus fairly well based.

Presence of similar glutinous dorsal tubercles in both *Ponera* and *Hypoponera* larvae might be supposed to indicate relationship between them. However, convergent evolution of similar tubercles is demonstrable in several ponerine genera. The following details are abstracted from my notes on larval characters and ponerine evolution. They contain some new information on genera, the larvae of which are undescribed. Detailed discussion will be presented elsewhere; in the meantime the papers of G. C. & J. Wheeler (1952) are essential references. I have conducted experiments in New Guinea and Panama with all genera named here. The specialized dorsal tubercles serve for attachment of the larvae to the nest walls, or even to the ceiling in moist or flooded conditions.

Paired doorknob-shaped tubercles, similar to those of *Ponera* and *Hypoponera*, are found in two other genera among the smaller Ponerini: *Cryptopone* Emery (sensu Brown 1963) has 4 or 5 pairs of these organs, on abdominal segments III–VI or III–VII inclusive. *Brachyponera* Emery has 3 pairs in young larvae, on abdominal segments II–IV. In older larvae (probably in the last 2 instars) these metamorphose into 2 flat transverse raised welts, which also serve for attachment of larvae to the walls of the nest.

Brachyponera may be related to *Hypoponera*, but *Cryptopone* is apparently on a separate line of descent from either *Ponera* or *Hypoponera*; its tubercles have almost certainly been convergently developed. Considering the evidence of adult characters, that *Ponera* and *Hypoponera* are not closely related, glutinous tubercles have been evolved at least three times in tribe Ponerini. Their presence, therefore, does not indicate relationship among the genera involved, but is probably correlated with reduced size and cryptobiotic nesting habits.

Similar homoplastic, but probably non-homologous, tubercles are present in larvae of genus *Myopias*. These are single, median, non-paired structures on the dorsa of abdominal

segments V and VI. *Myopias* is very distinctive, and clearly not closely related to the preceding genera. Probably homoplastic structures, similar to the welts of older *Brachyponera* larvae, are present in some members of genus *Anochetus* (tribe Odontomachini). Larvae of *Probolomyrmex angusticeps* M. R. Smith (tribe Platythyreini) have entirely distinctive glutinous organs, certainly not homologous with any discussed above. These are single and terminal on the abdomen, and are used to suspend the larvae, head downwards, from the nest ceiling (Taylor 1965).

In conclusion, mushroom or doorknob-shaped glutinous tubercles should not lightly be used as phylogenetic markers indicating relationship between ponerine genera; since such structures have apparently been evolved on at least six occasions in the subfamily. The fact that *Ponera* and *Hypoponera* have similar tubercles, arranged similarly, does not indicate relationship between them. There can be little doubt that this resemblance is convergent; of course it is not perfect, since all known *Hypoponera* have 2 pairs of these organs, while *Ponera* has a primary complement of 3 pairs, with 4 pairs present as a probably secondary character in one superspecies.

HYPOPONERA SPECIES, PHYLOGENY AND DISTRIBUTION

Hypoponera includes almost all species previously included in *Ponera*, except those assigned here to that genus. It probably contains about 100-120 species.

All New World material studied here (a total of about 2000 specimens) belongs in *Hypoponera*, apart from that reviewed below under *Ponera pennsylvanica* and *P. exotica*. All African and Madagascan specimens also belong here, except for a few *P. coarctata* specimens taken north of the Sahara. I have seen type or authentically type-compared material of all named Indo-Australian, Japanese and Oceanian "*Ponera*", and can confidently claim that all those not discussed as true *Ponera* species in the revision to follow belong in *Hypoponera* (or very occasionally elsewhere).

Several old *Ponera* species, *P. mjoergei* Forel and *P. typhla* Karawajew were removed recently to *Cryptopone* by Brown (1963). The two erstwhile African *Cryptopone* species, *angustata* Santschi and *hartwigi* Arnold, placed in *Ponera* by Brown (*loc. cit.*), actually belong in *Hypoponera*. There is much species-level synonymy in *Hypoponera*, and at least as many species as those currently valid remain undescribed in the material I have in hand. It would be useless to list now all species definitely assigned to the genus, since so many entries would be synonymous, numerous as-yet-undescribed species could not be included, and much of the proposed new synonymy requires discussion. Complete details will be published in forthcoming papers on the genus.

Hypoponera is virtually cosmopolitan in distribution, and includes a number of wide ranging tramp species, such as *H. gleadowi* (Forel), *H. punctatissima* (Roger), *H. eduardi* (Forel) and *H. opaciceps* (Forel). It is sparsely represented in the Holarctic regions, apart from a Japanese extension of the Oriental fauna, and seems to be poorly developed in India (this may be due to deficient collecting). If current indications are true, no autochthonous species are present in North America or Europe. The southern continents (including the Neotropical, Ethiopian, and Australian regions) and the Malayan parts of the Oriental region, have large endemic faunas. Specific records extend south to the Cape of Good Hope, to Tasmania, and at least to 40° S. lat. in Argentina. Apparently endemic

species occur on Ceylon, Madagascar, and the Fiji Islands; in the latter two areas some radiation has taken place, with several aberrant productions. There appear to be no native species in New Zealand, or in Polynesia, including the Samoan, Hawaiian and Galapagos groups, and no apparent endemics are known from the Atlantic or Indian Ocean Islands. Virtually no part of the tropical or warm temperate world is without tramp species; usually *H. gleadowi* or *H. punctatissima*. The taxonomic confusion existing in the genus is due, in large part, to the numerous synonyms of about six more or less widespread forms. The tramp species, incidentally, almost all have ergatoid males, a feature that may be associated with their success, through some kind of simplification of nuptial activity.

The African *Hypoponera* fauna contains a large number of small *Ponera*-like species assigned to the *abeillei* group. This is interesting, since true *Ponera* is absent south of the Sahara. These small African species also convergently resemble small *Cryptopone* species, with which some of them have been confused. Significantly *Cryptopone* also appears to be absent from Africa south of the Sahara (Brown 1963). In some areas where medium size Ponerini, such as members of the genera *Brachyponera* and *Mesoponera*, are scarce or absent, extremely large size species of *Hypoponera* may be present. This is so in parts of South America, the Fiji Islands and Madagascar. There is evidence that these large species have moved into the "adaptive zone" usually occupied by medium-size Ponerini of other genera.

Revisionary studies on ponerine ants, in process by W. L. Brown and myself, will not yet allow final decisions on intergeneric phylogenetic relationships. However, *Hypoponera* could be related to the complex of genera including *Mesoponera* and *Brachyponera*. Superficially many of its species resemble *Brachyponera*. However, members of that genus are generally larger, have a basal mandibular pit, relatively large eyes, and the oral palpi of all castes are less reduced. The winged forms have anal lobes on the hindwings, and the males have strong pygidial spines. It is possible that *Hypoponera* and *Brachyponera* are approximately cognate, and that most of the above characters have been lost or reduced in the descent of *Hypoponera*, in adaptive correlation with its reduced size.

SOME NEW COMBINATIONS IN HYPOPONERA. For the purpose of reference in the present paper the following *new combinations* in the genus *Hypoponera* are here formally declared. I have examined holotype or paratype material of all these species. Full synonymy will be given in forthcoming *Hypoponera* revisions. The originally assigned status is given in parentheses. (1) *H. abeillei* (André) 1881 (*Ponera*); (2) *H. angustata* (Santschi) 1914 (*Cryptopone*); (3) *H. biroi* (Emery) 1900 (*Ponera*); (4) *H. boerorum* (Forel) 1901 (*Ponera coarctata* subspecies) *new status*; (5) *H. camerunensis* (Santschi) 1914 (*Ponera abeillei* variety) *new status*; (6) *H. ceylonensis* (Mayr) 1897 (*Ponera*); (7) *H. eduardi* (Forel) 1894 (*Ponera*); (8) *H. gleadowi* (Forel) 1895 (*Ponera*); (9) *H. hartwigi* (Arnold) 1934 (*Cryptopone*); (10) *H. imatongica* (Weber) 1942 (*Ponera coarctata* subspecies) *new status*; (11) *H. mackayensis* (Forel) 1900 (*Ponera coarctata* subspecies) *new status*; (12) *H. monticola* (Mann) 1921 (*Ponera*); (13) *H. natalensis* (Santschi) 1914 (*Ponera coarctata* subspecies) *new status*; (14) *H. punctatissima* (Roger) 1859 (*Ponera*); (15) *H. queenslandensis* (Forel) 1900 (*Ponera*); (16) *H. scitula* (Clark) 1934 (*Ponera*); (17) *H. zwaluwenburgi* (Wheeler) 1933 (*Pseudocryptopone*).

EVOLUTION AND PHYLOGENY

In the systematic discussion below, the *coarctata* group is discussed first, followed by

treatment of the 26 Indo-Australian forms. These are arranged in seven species groups containing 2-5 species each, with five more or less distinctive forms considered independently.

Ponera alpha is apparently the most primitive species. It most closely resembles members of the genus *Ectomomyrmex* and the two endemic Australian "*Trachymesopus*" species, which are more generalized in structure than *Ponera* but appear to be related to it (see below). Moreover *alpha* possesses none of the features which could have been derived only by reduction or specialization in other species. The scapes are relatively long and the antenna lacks a segmentally differentiated club, the median clypeal tooth is distinct, the eyes are moderately well faceted, the sculpturation and pubescence unreduced, the mesosomal suturation complete, and the propodeum has strongly angled posterolateral edges. The node is contained by two complex strongly arched faces, a vertical anterolateral one and a transverse posterodorsal; these are separated by a strongly margined sinuate edge. This general form of the node is seen also in other genera of tribe Ponerini, including *Ectomomyrmex*, *Pachycondyla* and *Neoponera*; it almost certainly represents a primitive character within *Ponera*. In addition *alpha* is extremely large, and has a relatively broad head and petiolar node.

Starting with this species, and progressing through the Indo-Australian series, various general morphological tendencies are evidenced, including the following:

1. Reduction in size.
2. Decrease in relative breadth of head and petiolar node, and in relative length of antennal scapes.
3. Loss of median clypeal tooth and mesometanotal and lateral mesonotal sutures, and reduction of posterolateral propodeal angles.
4. Reduction in size of the eyes, and the number of their facets.
5. Reduction in pilosity, intensity of sculpturation, and darkness of color.
6. Modification of petiolar node by rounding of its angles and by disruption of the single primitive posterodorsal face into separate posterior and dorsal ones, so that the node assumes a more oblong structure.
7. Modification of terminal part of antennal funiculus to form a 4- or 5-jointed club.

These tendencies run parallel through the series of species, and thus have a sequential orientation relative to one another. Their phylogenetic polarity can be determined by (1) considering the characters of *alpha* to be generally primitive and (2) by the fact that certain tendencies have an intrinsic polarity; since one extreme could only have been derived from the other. For example, a complete mesosomal sutural complement is clearly primitive; as are long scapes, non-clubbed antennae, and the presence of a median clypeal tooth, at least in this section of the tribe Ponerini. The fact that most modifications are correlated with reduction in overall size is significant. Parallel morphoclines associated with size decrease are found also in *Hypoponera*, especially in the *abeillei* group, and such tendencies as the modification of petiolar node structure, reduction of the eyes, and loss of the median clypeal tooth are evidenced also in *Ectomomyrmex*.

The pattern of evolution does not follow a series of straight-line morphoclines in these characters, but the structural losses, reductions, and gains have all apparently occurred several times in the history of the genus. For example, loss of the median clypeal tooth is extremely irregular from group to group, the mesometanotal suture has been independently lost at least four times (in *P. selenophora*, *P. scabra* and the groups of *taipingensis* and

tenuis). Vestiture has been almost entirely lost in several unrelated species (*elegantula* and *clavicornis*), and tendencies towards development of an antennal club are present in several groups. Various "countercurrent" trends are implied: the sculpturation of *P. clavicornis* is greatly intensified over that of its nearest relatives, the eyes are apparently secondarily enlarged in the *elegantula* group and in *P. woodwardi*, and the latter species has secondarily elongated scapes. One peculiar form, *P. manni*, has evidently become secondarily enlarged in size, and in so doing has developed a much broader head and longer scapes than its apparent relatives. Several "new characters" are seen in the acquisition of an extra fourth pair of glutinous abdominal tubercles in larvae of the *coarctata* group, and the loss of pupal cocoons in *P. tenuis*. In females the wing venation has been modified similarly in two unrelated species, *chapmani* and *swezeyi*. Reduction of the male palpal formula from 5:3 to 2:2 or some intermediate condition has evidently been very irregular.

The following relationships among the species are indicated. *P. selenophora* is essentially a smaller, slightly modified version of *alpha*. The groups of *scabra*, *sinensis* and *taipinensis*, are at about the same structural grade; with their approximate degree of specialization following the order listed. Within this series reduction in size, narrowing of the head and node, and modification of petiolar form, ocular reduction, shortening of the scapes and loss of the mesometanotal suture are evidenced, and there is a tendency towards indistinct differentiation of an antennal club. The *elegantula* group is apparently cognate with these three groups, and seems to represent a line derived from *selenophora*-like stock, marked primarily by secondary enlargement of the eyes. The groups of *japonica*, *leae* and *tenuis*, appear to be related and derived from the preceding series of groups through *japonica*-like stock. *P. clavicornis* is rather distinctive and probably cognate with the base of this line, and *P. manni* is evidently an aberrant offshoot from *japonica*-like stock. The *coarctata* group probably originated close to the ancestors of the *japonica* group. Among the smaller Indo-Australian species the groups of *leae* and *tenuis* may be related, by virtue of their mutual possession of 4-segmented antennal clubs, opposed to the 5-segmented structure in the *japonica* group. The *tenuis* group is presumably derived from *leae*-like stock by loss of the mesometanotal suture.

Ponera could be related to *Ectomomyrmex*, the characters of which are discussed by Brown (1963). *Ectomomyrmex* species are generally similar to *P. alpha*, but they have less reduced oral palps, in all castes; the workers have the mesepisternum divided by a horizontal suture, and the posterior faces of the propodeum and node have highly characteristic heavy vertical or transverse striations. Vestigial traces of such sculpturation could be present in *P. alpha*, as detailed in its description below. *Ectomomyrmex* alates have anal lobes on the hindwings, and the larvae lack dorsal abdominal "doorknob" tubercles.

Even closer affinities may lie with the two endemic Australian "*Trachymesopus*" species, *pachynodus* (Clark) and *rufonigra* (Clark). These are somewhat similar to *Ectomomyrmex* but lack the peculiar propodeal and nodal sculpturation and the horizontal mesepisternal suture. They look like large *Ponera* species, but the palpal formula of the female castes is 3:3, the alates have anal lobes on the hindwings, and the male gonoforceps are unlike those of *Ponera*. Structure of the female subpetiolar process is possibly significant; it lacks a fenestra, but has paired posterolateral teeth like those of *Ponera*.

GEOGRAPHICAL DISTRIBUTION

There are two geographical groups of *Ponera* species; most are Indo-Australian, but the *coarctata* group is amphiatlantic.

The Indo-Australian species apparently have their evolutionary center in New Guinea, although this may ultimately shift westwards to SE Asia as knowledge of the genus increases. There is a single E. Australian endemic, *P. leae*, occurring south to Tasmania. Apparently endemic species are also present on Fiji and the Samoan Is. The natural range of the genus evidently does not include New Zealand, although a presumably introduced local population of *P. leae* is known from North Island. There are endemic species, with New Guinean or Asian affinities, on the Philippines, and the Japanese *P. scabra* is related to one of these. The second Japanese species, *P. japonica*, is probably widespread in the Orient since it occurs in Malaya and Java.

The members of the *coarctata* group are closely related, and clearly cognate. There can be little doubt that they represent descendants of an amphiatlantic ancestor and that their speciation has taken place in isolation on either side of the Atlantic. Their ancestors may have spread from Europe to America (or the reverse) across the N. Atlantic, not across Siberia and the Bering Straits as seems usually to be the case. This notion may be changed with knowledge of the males and immatures of *P. japonica*. The primary characters of the *coarctata* group include larval and male structures, and these stages are not known for *japonica*, which is possibly close to *coarctata*. *Ponera* has been present in Europe at least since Baltic Amber times; since an extinct species, *P. atavia*, is known from the Amber.

Perhaps the most important single factor in the zoogeography and evolution of the genus has been the attainment of small size by certain species. These include members of the *japonica*, *leae* and *tenuis* groups. Almost every known species with head width less than 0.45 mm is widespread. *P. leae* ranges from eastern Australia to Tasmania and New Zealand, New Caledonia and Norfolk Island, and the related *P. exotica*, known from several widely separated parts of the SE United States, is almost certainly a Melanesian species. These species have doubtless been assisted in dispersal by man.

Other small sized wide-ranging species include *incerta* and *tenuis*, which are evidently New Guinea based. The former is, however, not known from New Guinea but ranges from Java to Samoa, and north to Micronesia. The latter is known from New Guinea, Micronesia and Samoa, but has not been taken in eastern Melanesia. *P. swezeyi*, the smallest known species, is found on Samoa and the Hawaiian Islands. The dispersal powers of these species have no doubt been enhanced by their small size and cryptobiotic habits, and it is probable that Polynesian or European man may have carried them extensively, especially in soil attached to the roots of crop plants.

The basic attributes of the "taxon cycle" of Melanesian ants as discussed by Wilson (1958, 1959) are demonstrated by *Ponera* species. "Stage 1" forms include *alpha* and *xenagos*, *elegantula* and *augusta*, *syscena* and the species of the *P. szentivanyi* complex. "Stage 2" species include *incerta* and *tenuis*, *clavicornis* and *selenophora*. Peripheral species derived from ancestral stock probably of New Guinean origin ("Stage 3") include the Fijian *colaensis* and the Samoan species *loi* and *woodwardi*, also *swezeyi*, and *borneensis*. Several New Guinea based species, *clavicornis* and *selenophora*, are found in Australia; they are apparently limited to lowland rain forest at the extreme tip of Cape York.

ECOLOGY AND BEHAVIOR

These ants are essentially cryptobiotic, nesting in rotting logs in forested areas, or under stones in nonforested situations. In the tropical areas specimens are rarely encountered away from rain forest. In temperate areas, however, species may occur in relatively lightly forested areas. This appears to be the case with *japonica*, *pennsylvanica* and especially with *coarctata*. The Australian *P. leae* is essentially limited to rain forest in the northern parts of its range, but further south it may be found in dry, lightly forested areas. Foraging is probably cryptobiotic, though some New Guinea species have been taken straying on the ground surface.

Little information is available concerning feeding. However, most species are probably insectivorous. I have conducted feeding experiments with some of the New Guinea and Samoan species, including *xenagos*, *elegantula*, *tenuis*, *incerta* and *woodwardi*. These were unsuccessful with the larger species, except *elegantula*, which accepted moderately large (8–12 mm) campodeid and japygid Diplura. *Tenuis* and *incerta* accepted smaller (4–6 mm) campodeids, isotomid and sminthurid Collembola, and small newly hatched spiders (2 mm long). Negative feeding response was obtained with eggs and larvae of various ants, small crushed insects of various orders, and small myriapods. Stray workers were never observed carrying prey, and distinct middens of insect or other remains were not located near nests.

Colonies usually contain about 30 workers. Larvae and pupae are not segregated in most cases, but occasionally aggregations of pupae were observed. These may have included the total brood of the colonies involved. Larvae are attached to the floor or walls of the nest galleries by the glutinous abdominal tubercles described above, and the ants move them high up on the walls or ceilings of artificial nests, if they are flooded. Details of nuptial behavior of *pennsylvanica* were given by Wheeler (1900), and Haskins & Enzmann (1938). The flights appear to be of a pattern typical for ants, with the alates meeting in the air and mating there or on the ground. Colony foundation is non-claustral and independent in *pennsylvanica* (Kannowski 1959); judging from my observations this is typical for the genus.

Interspecific competition between *tenuis* and *incerta* has been studied in Samoa. This work is reported below under the heading of the latter. The species *loi* and *woodwardi* of Samoa, are limited to high elevations and may have retracted their ranges due to competition with the introduced *Hypoponera confinis*, which is abundant at low elevations.

TAXONOMIC CHARACTERS, MEASUREMENT, TECHNIQUES

Taxonomically *Ponera* has two significant features: amazing uniformity of general habitus; and almost total lack of meristic or discontinuous characters. The few meristic features include the mandibular dentition, the number of eye facets, and the number of segments in the funicular club (if one is differentiated). In most cases citation of these characters must include qualifying expressions such as "indistinctly" or "apparently." Ostensibly discontinuous characters include presence or absence of a median clypeal denticle, a segmentally differentiated antennal club, or the mesometanotal and lateral mesonotal sutures. While these characters allow indubitable placement of some species into sets with the character either present or absent, there are species with ambiguous or variable expression of one or more of them. In addition, few characters can be held to have been gained or lost only once in the history of the genus. Perhaps the most meaningful characters for

taxonomic discrimination are those involving the standard measurements and indices detailed below. Use of these measurements is *essential* for the proper systematic study of small Ponerine ants. Indeed, the characteristic attributes of most *Ponera* species are reflected in their measurements and indices.

An ocular scale reading 0.1 and 0.01 mm was used for measurement. The measurements vary in "quality", because intrinsic differences between the subject structures affect the accuracy which can be expected. Head width, head length and petiole height are the most "repeatable"; while scape length and petiolar node length are the least so (maximum error here, however, would rarely exceed 0.005 mm).

The following standard measurements and indices are used below:

Head length (HL): Maximum measurable length of head, in full face view, from mid-point of occipital border to anteriormost point on anterior clypeal border (to the apex of the median clypeal tooth if one is present). The upper basal edge of the labrum occasionally projects beyond the median anterior clypeal border; it should not be included in this measurement.

Head width (HW): *Worker and* ♀. Maximum measurable width of head, in full face view, excluding eyes. ♂. Maximum measurable width of head, across and including eyes.

Scape length (SL): Maximum length of scape, not including its articulation condyle.

Cephalic index (CI): $(HW \times 100)/HL$.

Scape index (SI): $(SL \times 100)/HW$.

Pronotum width (PW): Maximum width of pronotum, from directly above, measured at right angles to long axis of mesosoma.

Petiole height (PH): Maximum measurable height of petiole, in lateral view, from summit of node, to extreme lowermost part of subpetiolar process.

Petiolar node length (PNL): With petiolar segment viewed exactly from the side; the distance from the midpoints of the curves where the anterior and posterior faces of the node meet its anterior and posterior peduncles.

Dorsal petiole width (DPW): Maximum width of petiolar node, in dorsal view, measured at right angles to body axis.

Petiolar node index (PNI): $(\text{Dorsal Petiole Width} \times 100)/PW$.

Lateral petiolar index (LPI): $(PNL \times 100)/PH$.

Ocular index (sexuals only): Maximum diameter of eye expressed as a percentage of head width.

Weber's length of mesosoma (WL) (♂♂ only): Diagonal distance from anterior pronotal margin (exclusive of its frontal "collar") to maximum extension of posterolateral meta-pleural lobe, measured in side view.

Measurement of sculptural dimensions: Where numerical values are cited for punctural diameters, etc., they have been determined by use of ocular scales yielding units of 0.01, 0.0075, and 0.005 mm.

Determination of posterior extension of scape: Span of the scape, relative to the *median* occipital border, is stated for most species. To determine this a drop of relaxing fluid is allowed to flood the head of the specimen, while under the microscope. Before the fluid

evaporates the scape may be articulated to lie back parallel to the long axis of the head, usually adherent to the frons. The ocular measuring scale is used to determine the degree to which the scape exceeds, or fails to exceed, the occipital margin, relative to its maximum thickness.

Citation of palpal formula: Palpal formulae are given with a statement indicating whether they were recorded from dry specimens ("by inspection"), or from disarticulated mouthparts ("by dissection"). Formulae are not given without qualification unless "certainly" correct; nevertheless, those obtained by dissection are considered the most dependable.

KEY TO SPECIES OF PONERA

(Based primarily on workers; where applicable ♀, ♂, or larval characters are included. The alate castes are too poorly known to allow presentation of separate keys.)

1. An exceptionally large species (HW 0.76–0.85 mm); petiolar node relatively very broad (PNI 92–98). (NE New Guinea) **alpha***
- Smaller species (HW less than 0.73 mm); petiolar node narrower (PNI less than 90) 2
- 2 (1). Eyes large, with 9–16 distinct facets; medium size species, HW 0.55–0.62 mm; ranges for CI and SI 80–93, and 86–91 respectively 3
- Eyes smaller, usually with less than 6 facets; one or more of the relevant dimensions outside the ranges specified above [one species (*P. woodwardi*) has eyes with 7–11 facets, but it has CI 77–81, SI 98–102] 5
- 3 (2). Larger species (HL 0.70–0.74 mm); head relatively narrow (CI 80–83); mesosoma completely devoid of standing hairs. (Mountains of NE New Guinea) **elegantula** Wilson
- Smaller species (HL 0.60–0.65 mm); with proportionately broad heads (CI 86–93); mesosoma with distinct erect pilosity 4
- 4 (3). Relatively broad-headed species (CI 90–93); petiolar node proportionately narrow (PNI 81–83). (Mountains of NE New Guinea) **augusta***
- Head relatively narrow (CI 86–88); petiolar node broader (PNI 86–90). (Mountains of C. Borneo) **borneensis***
- 5 (2). Relatively large, broad-headed species, with the following combination of characters—HW 0.61–0.70 mm, HL 0.75–0.84 mm, CI 78–98, petiole height 0.50–0.59 mm 6
- Usually much smaller species, with a very different array of dimensional ranges; those with HW measurements falling within the above range, have at least two of the other dimensions outside the ranges given 8
- 6 (5). Head relatively broad (CI 86–90); median clypeal tooth represented at most by a low tumosity; PNI values ranging 77–84. (NE New Guinea) .. **xenagos** Wilson
- Head narrower (CI 78–84); median clypeal tooth usually distinct—if it is vestigial the PNI exceeds 84 7
- 7 (6). Head relatively broad (CI 83–84); scapes clearly exceeding median occipital border when laid back along head; node relatively narrow (PNI 79–80) (Mindanao, Philippines) **chapmani***

* New species

- Head less broad (CI 78-83); scapes slightly but distinctly failing to reach median occipital border; node relatively broad (PNI 84-89). (Honshu, Japan)..... **scabra** Wheeler
- 8 (5). Head relatively broad, CI 88-95 9
 Head not so broad, CI never exceeding 86, usually much lower..... 12
- 9 (8). Smaller species (HW 0.47-0.51 mm), PNI values ranging 82-85 10
 Larger species (HW 0.57-0.65 mm), PNI values outside range cited above (higher or lower) 11
- 10 (9). Smaller species (HW 0.47-0.51 mm, HL 0.50-0.54 mm), with relatively broad head and short scapes (CI 92-95, SI 78-81). (Negros I., Philippines).....
 **oreas** (Wheeler)
 Known only from unique holotype. Larger species (HW 0.54 mm, HL 0.61 mm), with narrower head and longer scapes (CI 89, SI 83). (Hong Kong)
 **sinensis** Wheeler
- 11 (9). Petiolar node relatively high and broad (petiole height 0.45-0.48 mm, PNI 85-89); color dark brown, almost black; eyes with 2-3 facets; size slightly larger (HW 0.59-0.65 mm). (NE New Guinea; Cape York, Australia)
 **selenophora** Emery
 Petiolar node relatively low and narrow (petiole height 0.41 mm, PNI 73 in unique holotype); color medium reddish brown; eyes with single, very minute facets; HW slightly lower (0.57 mm). (Viti Levu, Fiji) **manni***
- 12 (8). Mesometanotal suture not incised on mesosomal dorsum.....13
 Mesometanotal suture distinctly incised on mesosomal dorsum..... 22
- 13 (12). Petiolar node relatively narrow (PNI 65-76); size small (HW 0.30-0.45 mm)... 14
 Petiolar node relatively broad (PNI 78-91); larger species (HW 0.48-0.63 mm, with one exception, *P. clavicornis*, HW 0.43-0.47 mm)..... 17
- 14 (13). Larger species, HW 0.39-0.45 mm. (New Guinea and Samoan Is.)...**tenuis** (Emery)
 Much smaller species, HW 0.30-0.34 mm..... 15
- 15 (14). Slightly smaller species (HW 0.30-0.32 mm), with proportionately short scapes (SI 78-83); petiolar node narrow (PNI 61-65). (E. New Guinea)...**szaboi** Wilson
 Slightly larger species (HW 0.32-0.34 mm), with proportionately long scapes (SI 88-94); petiolar node broader (PNI 72-86).....16
- 16 (15). Lateral surfaces of mesosoma very feebly shagreened to smooth and shining; petiolar node relatively low, its height in the unique holotype 0.25 mm, about the same as the pronotum width; the SI 88. (NE New Guinea)...**petila** Wilson
 Lateral surfaces of mesosoma all moderately shagreened, and opaque; petiolar node relatively high, its height in the single measurable specimen 0.29 mm, or slightly more than the pronotum width; the SI 94. (SE New Guinea)...
**szentivanyi** Wilson
- 17 (13). Moderately small species (HW 0.43-0.47 mm); mesosomal dorsum in profile completely lacking erect hairs. (New Guinea and E. Melanesia)...**clavicornis** Emery
 Larger species (HW 0.50-0.63 mm); mesosomal dorsum in profile with abundant standing hairs..... 18
- 18 (17). Scapes exceptionally long, exceeding median occipital border by 1 to 1.5× their maximum thickness (SI 98-102). (Upolu, Samoan Is.)..... .. **woodwardi***
 Scapes usually approximately contiguous with median occipital border, rarely

- clearly exceeding it, SI always less than 92, usually considerably so 19
- 19 (18). Petiolar node relatively broad (PNI 84-91) 20
 Petiolar node proportionately narrow (PNI 78-82) 21
- 20 (19). Head relatively broad, petiolar node relatively narrow (CI 84-86, PNI 84-85).
 (Malaya) **taipingensis** Forel
 Head proportionately narrow, node relatively broad (CI 81-83, PNI 88-91).
 (Fiji Is.) **colaensis** Mann
- 21 (19). Slightly smaller species (HW 0.48-0.50 mm, HL 0.60-0.62 mm), lacking a distinct median clypeal tooth. (New Guinea) **syscena** Wilson
 Slightly larger species (HW 0.51-0.58 mm, HL 0.62-0.70 mm), with a distinct strong acute median clypeal tooth. (Upolu, Samoa) **loi***
- 22 (12). Smaller species (HW usually less than 0.40 mm, HL less than 0.50 mm—one Japanese and Oriental species with HW 0.42-0.50 mm, and HL 0.53-0.63 mm).
 Larvae, when known, with 3 pairs of dorsal glutinous tubercles; ♂ palpal formula 4 : 2 or 2 : 2 23
 Larger species (HW 0.50-0.63 mm, HL 0.64-0.77); larvae with 4 pairs of glutinous tubercles on abdominal dorsum; ♂♂ with 5 : 3 palpal formula. (Europe and E North America) 27
- 23 (22). Antennal funiculus with an indistinctly to distinctly differentiated 5-segmented club; HW 0.32-0.50 mm 24
 Antennal funiculus with a distinctly 4-segmented club; HW 0.36-0.41 mm 26
- 24 (23). Size larger (HW 0.42-0.50 mm, HL 0.53-0.63 mm); median clypeal tooth present in some populations. (Japan, Malaya and Java) **japonica** Wheeler
 Size smaller (HW 0.32-0.40 mm, HL 0.42-0.50 mm); median clypeal tooth never developed 25
- 25 (24). Larger species (HW 0.36-0.40 mm); head relatively broad (CI 78-84). (Java, E. Melanesia, Samoa) **incerta** (Wheeler)
 Smaller species (HW 0.32-0.33 mm); head relatively narrow (CI 76-78). (Samoa and Hawaii) **swezeyi** (Wheeler)
- 26 (23). Either the HW is 0.35 mm or less, or the CI is 79 or greater, or both. Where neither of these characters is shown the LPI is within the range 52-57. (SE United States—probably introduced) **exotica** M. R. Smith
 Either the HW is 0.42 mm or greater, or the CI is 76 or less, or both. Where neither character is shown the LPI range is 59-67. (E. Australia, New Zealand, Norfolk I., New Caledonia) **leae** Forel
- 27 (22). Disc of pronotum moderately shining, with a scattering of fine point-punctures, spaced at intervals of 2-3× their average diameter; petiolar node of queen relatively narrow (PNI 63-66). (Europe, NW Africa, Middle East)
 **coarctata** (Latreille)
 Disc of pronotum subopaque, with a close cover of moderately coarse punctures about 0.005 mm in diameter, separated by distances equal to about 0.5× their average diameter; petiolar node of queen much broader (PNI 76-80). (E North America) **pennsylvanica** Buckley

A. SPECIES OF EUROPE AND NORTH AMERICA

Ponera coarctata Group

This group contains a closely related amphiatlantic species pair: *P. coarctata* (Latreille) of Europe, the Middle East and North Africa; and *P. pennsylvanica* Buckley, of E North America. It is distinguished mainly by the fact that the larvae have 4 pairs of glutinous tubercles on the abdominal dorsum, whereas all known Indo-Australian species have 3 pairs. The workers are medium to dark brown in color and of about medium size for the genus (head width 0.50–0.63 mm). The median clypeal denticle is vestigial but there is a longitudinal carina. The eyes are small, no antennal club is differentiated, and the mesometanotal suture is distinctly incised on the mesosomal dorsum. Members of the Indo-Australian species groups of *sinensis*, *taipingensis* and *elegantula* are similar in size to *coarctata* and *pennsylvanica*. However, the heads of the *sinensis* group species are broader (worker cephalic index 89–95 as opposed to 77–85 in the *coarctata* group); workers of the *taipingensis* group lack an incised mesometanotal suture; and those of the *elegantula* group have much larger, more highly faceted eyes.

The females are normal for the genus, and have “*coarctata* type” wing venation. Males have a 5 : 3 palpal formula. Most known Indo-Australian *Ponera* males have a 2 : 2 palpal formula as in the female castes, but 4 : 2 and 3 : 2 formulae are known respectively in *incerta* and *oreas*.

The extinct *P. atavia* Mayr, of the Baltic Amber, is apparently allied to these forms, and has been included in the *coarctata* group with them.

1. *Ponera coarctata* (Latreille) Figs. 4, 15–17, 21.

Formica coarctata Latreille, 1802, Bull. Soc. Philom. Paris 3: 65, pl. 3, fig. 1, worker, ♀.

Original localities: Luxembourg; Gentilly, France.

Formica contracta Latreille, 1802, Histoire Naturelle des Fourmis, p. 195, pl. 7, fig. 40, worker, ♀, distribution.

Ponera contracta: Latreille, 1805, Hist. Nat. Crust. Ins. 13: 257.

Ponera coarctata: Dalla Torre, 1892, Wien. ent. Ztg. 11: 93; 1893, Cat. Hym. 7: 38.

Ponera coarctata var. *atlantis* Santschi, 1921, Boll. Soc. Espan. Hist. Nat. 21: 166, fig. 2, worker. Original localities: Algeria and Tunisia. (Syntypes examined—Santschi coll.)

New Synonymy.

Ponera coarctata coarctata colchica Arnoldi, 1932, Zool. Anz. 98: 63, worker. Original localities: Batu and Tsichis-Tsiri, U. S. S. R. **New Synonymy.**

Ponera coarctata var. *crassisquama* Emery, 1916, Rend. R. Acc. Sci., Bologna n. s. 10: 45, fig. 1, worker, ♀. Original localities: Italy and Tunisia. **New Synonymy.**

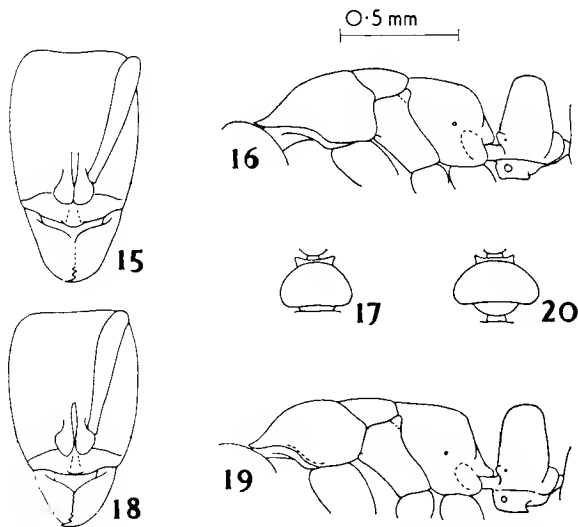
Ponera coarctata var. *lucida* Emery, 1898, Finska. Vet. Soc. 20: 7, worker. Original locality: Lenkoran, Azerbaijan, U. S. S. R. **New Synonymy.**

Ponera coarctata var. *lucidula* Emery, 1909, Deuts. Ent. Zeit. 1909: 370, worker. **New Synonymy.**

Ponera coarctata taurica Arnoldi, 1932, Zool. Anz. 98: 65. **New Synonymy.**

Ponera coarctata var. *testacea* Emery, 1895, Mem. Acc. Sci. Bologna (5) 5: 294, worker, ♀. Described from localities in Spain and Corsica. **New Synonymy.**

SYNONYMY. Like many European organisms *Ponera coarctata* has a long history of usage and has accumulated a number of synonyms. Some of these may be eliminated on purely



Figs. 15-20. Group of *Ponera coarctata*. *Ponera coarctata* (Latr.) worker (Fontainebleu, France): 15, head; 16, mesosoma and node; 17, node, dorsal view. *Ponera pennsylvanica* Buckley, worker (Giant City, Illinois): 18, head; 19, mesosoma and node; 20, node dorsal view.

nomenclatural grounds. *Contracta* is a simple objective junior synonym of *coarctata*; it was suggested by Latreille (1802b) as a more desirable replacement for the latter, which he had published earlier in the same year. His procedure was of course invalid, and *coarctata* holds priority. Notwithstanding, "*contracta*" was used almost exclusively by authors up to the time of Dalla Torre's *Catalogicus Hymenopterum* (1893), which lists 47 examples of its use and has only two citations for *coarctata*.

P. lucidula and *taurica* were both inadvertently promulgated; the former by Emery, in error for his *lucida*, and the latter was suggested by Arnoldi (1932) as a possible varietal name for some Taurischen specimens which he himself formally placed under Emery's variety *testacea*. Various subsequent authors

have perpetrated *lucidula*, in spite of Emery's correction published in the *Genera Insectorum*, fasc., 118 (1911).

The name *colchica* Arnoldi may be considered as an invalid infrasubspecific name, since it was originally assigned as the last name in a tetranominal form (see the *International Code of Zoological Nomenclature*, Rule 45c).

The remaining names listed in the above synonymy, *atlantis* Santschi, *crassisquama* Emery, *lucida* Emery, and *testacea* Emery, were all originally proposed as "varieties" under *coarctata*. As pointed out below there is little true geographical variation in *coarctata*, and there is no justification for the recognition of geographical races, whether or not one considers that they should be named as subspecies. However, there is considerable variation among local samples of the species, probably due to the production of eco- or ecophenotypes, and to intranidal allometric differences among the workers. All of the above forms are said to be of lighter color and less distinct sculpturation than the "typical" *coarctata*, and differences in the lateral and dorsal profiles of the petiolar node have been itemized. These features are precisely those which vary in local series, and there can be no grounds for retaining any of the above names. The uselessness of these varietal categories is well demonstrated by the papers of Kratochvil (1944) and Arnoldi (1932) who attempted to apply them to variant types among samples which clearly included members of the same or closely associated populations. It is clear from the published context that

the authors of several of these names were fully aware that the forms under discussion were mere local variants. It is also noteworthy that Emery did not assign type-specimens for his varietal names, judging from material now in his collection.

Other names were originally proposed as "subspecies" of *coarctata*. These include *boerorum* Forel (South Africa), *mackayensis* Forel (Australia), *natalensis* Santschi (Natal), and *imatongica* Weber (Sudan). I have examined the types of these forms, and find that all are referable to the genus *Hypoponera*.

Removal of *boerorum* and *mackayensis* from *Ponera* disposes of the zoogeographical confusion occasioned by Forel's having placed them as subspecies of *coarctata*. Mention of the resulting anomalous distribution pattern has been made in various works, including Creighton (1950), and a map of the ranges of these and other *coarctata* "subspecies" was unfortunately published by Lindroth (1957) in his fine study on trans-North Atlantic faunal connections. Past discussions accepting these forms as valid geographical races of *coarctata* are of course untenable.

The erstwhile subspecies *pennsylvanica* Buckley, of E North America is considered here to be a distinct, though closely related, species of *Ponera*, which is discussed below.

DIAGNOSIS. Characters distinguishing this species and its nearctic cognate *P. pennsylvanica* from other members of the genus are given under the species group heading above. The diagnostic features separating *coarctata* and *pennsylvanica* involve sculpturation in the worker and ♀ castes, the form of the petiolar node in ♀♀, and differences in the ♂ pygidial structure.

Worker: The following notes are based on several hundred specimens from most parts of the species range, distributed as shown by closed circles on the accompanying map (fig. 21).

No significant geographical variation is detectable in the standard dimensions and indices which are HL 0.67–0.77 mm; HW 0.50–0.60 mm; SL 0.47–0.57 mm; CI 77–82; SI 87–98; PW 0.39–0.46 mm; PNL 0.22–0.25 mm; PH 0.38–0.48 mm; DPW 0.29–0.36 mm; PNI 67–82. General form as shown in figs. 15–17. Mandibles triangular, with 3 large teeth occupying apical 1/3 of masticatory border, followed by a regular series of 9–14 minute denticles. Clypeus slightly produced anteriorly, with a rather distinct raised longitudinal carina — probably a vestige of the median tooth, seen in some Indo-Australian species. Scapes usually with their apices approximately contiguous with median occipital border, but they may fail to attain it by up to 1/3 their maximum thickness. Funiculus lacking a segmentally differentiated club, antennomeres increasing regularly in length and breadth towards apex which is moderately incrassate; apical segment a little longer than 2 preceding together. Palpal formula (several specimens dissected); *Maxillary* 2; *Labial* 2. Eyes small, with 1–5 very indistinct minute facets, situated about 0.85× the distance from lateral occipital border to midpoint of anterior genal border. Mesometanotal suture clearly incised on mesosomal dorsum, lateral mesonotal suture less distinct. A small lobate projection present on posterodorsal corner of the mesepisternum, usually separated from it by a fine suture-like trace. Posterolateral propodeal angles not raised, forming blunt angles of about 90° when viewed from above. Node in profile as in fig. 16, subpetiolar fenestra small, circular, posterodorsal teeth small but distinct. Dorsal surface of node, viewed from above, forming distinctly less to slightly more than a half-circle.

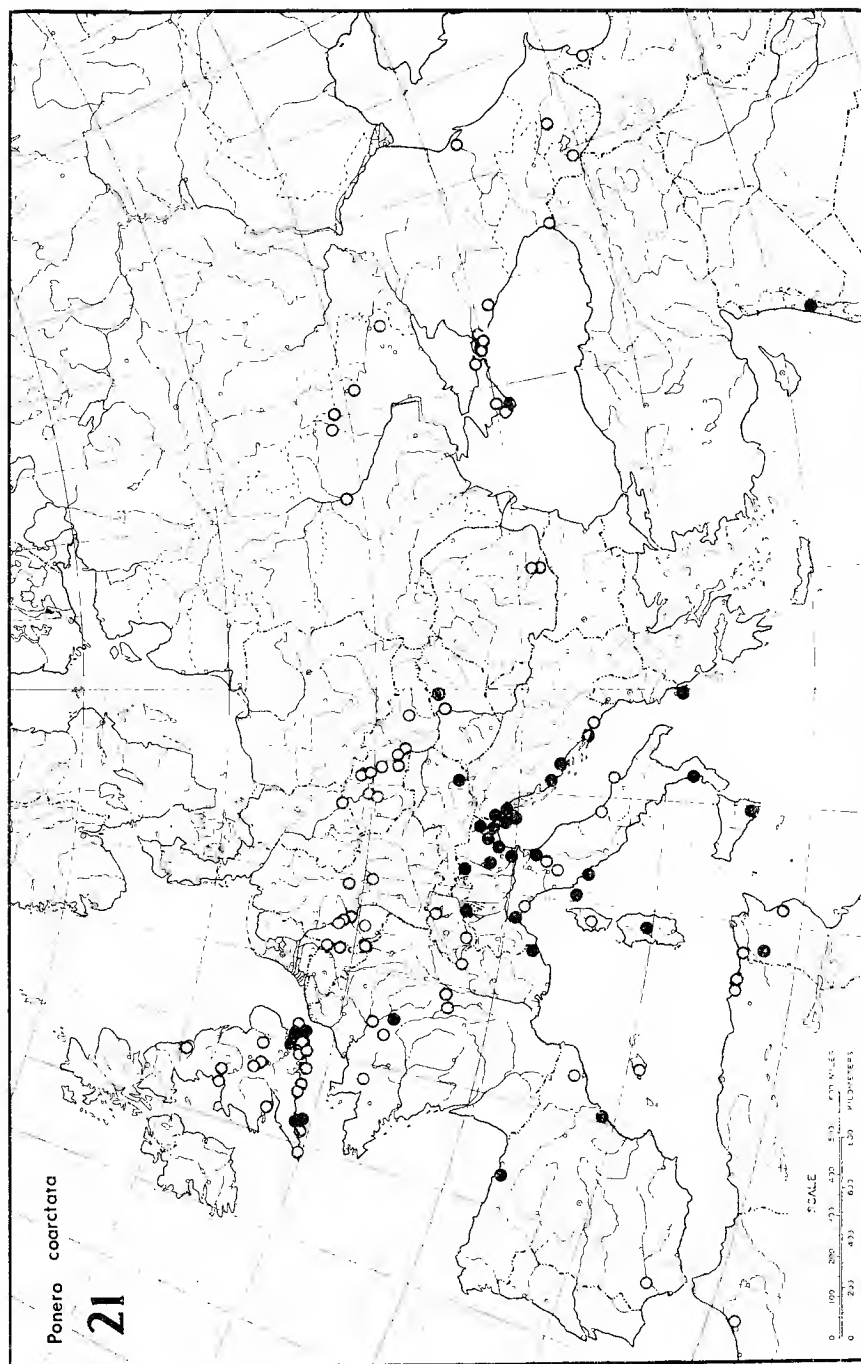


Fig. 21. *Ponera coarctata* (Lar.), Distribution. See text for explanation.

Mandibles smooth and shining, with a few scattered punctures, about 0.005 mm in diameter, separated by intervals equal to about $1/2$ their average diameter. Scapes moderately shining, with a cover of fine punctures, spaced at about their average diameter. Pronotum moderately shining, with a scattering of fine point-punctures, spaced at $2-3\times$ their average diameter. Mesonotum, dorsum of propodeum and sides of mesosoma less densely punctate, and quite strongly shining. Virtually no trace of longitudinal striation on lower mesepisternum and metepisternal area. Declivitous face of propodeum smooth and shining. Node and gaster feebly punctate, moderately shining.

Short erect to sub-erect pilosity and fine pubescence everywhere abundant — the pilosity of the clypeus, frontal lobes, dorsa of propodeum and node, and apex of gaster relatively long. Color ranging from light golden brown to a dark reddish mahogany hue. Mandibles, clypeus, antennae, coxae, and tip of gaster lighter — dull yellowish brown; remaining parts of legs yellowish.

There is little appreciable geographic variation in *P. coarctata* workers, except that those from the Mediterranean parts of its range tend to average slightly smaller than those from more northern locales, and to have somewhat lighter coloration. The smaller size specimens in each sample show various allometric differences from larger samples. Similar intranidal variation is seen in *P. pennsylvanica*, discussed below. Head length and scape length are negatively allometric relative to head width ($k=ca\ 1.4-1.45$), petiolar node width is positively allometric ($k=ca\ 0.7$), while pronotum width and petiole height are approximately isometric. Thus small specimens tend to yield higher values for scape index and petiolar node index, and lower values for cephalic index than do large ones. In addition petiolar node length is negatively allometric relative to petiole height, so that small workers tend to have bulkier petiolar nodes than large ones; these appear thicker in side view and the dorsal faces more closely approximate a half-circle in extent than do those of large specimens. Smaller specimens tend to be slightly lighter in color, and less hirsute than large ones, and to have the sculpturation a little less intense. There is sufficient variation in color within single samples to suggest that the callow period may be prolonged in this species.

The apparent tendency for color to be less intense in Mediterranean samples, may be correlated with the generally drier conditions there than in the north. The Australian *P. leae* Forel is known to produce small, relatively light colored, eco-types in the drier habitats in which it is found around Sydney. This could well be the case in *coarctata*, for certain of the Mediterranean samples are of normal dark coloration, and may be from more moist habitats than those usually occupied in this area.

♀. (fig 4). 11♀♀ from Italy, France and England, have the following measurements: HL 0.34-0.38 mm; HW 0.28-0.32 mm; SL 0.23-0.29 mm; CI 85-88; SI 84-86; PW 0.23-0.27 mm; PNL 0.11-0.13 mm; PH 0.21-0.24 mm; DPW 0.16-0.20 mm; PNI 63-66; maximum diameter of compound eye 0.07-0.10 mm; ocular index 24-28. Palpal formula (3 specimens dissected): *Maxillary* 2; *Labial* 2, as in the worker. General characters much as in *P. pennsylvanica*, but smaller in size, as indicated in above dimensions. Note that there is no overlap in the ranges of the 2 species for PW, PH, DPW, WL, and PNI. Females of *P. coarctata* are readily distinguished from those of *P. pennsylvanica* on the basis of these characters, and in addition the sculpturation is much less intense. Mandibles, clypeus, scapes, and front of head as in worker, the latter with punctures slightly

larger. Mesosomal dorsum moderately shining, with a scattering of small punctures about 0.005 mm in diameter, separated by distances equivalent to 1-2 \times their maximum diameter. These punctures more distinct on scutellum than elsewhere. Sides of mesosoma slightly less heavily punctured than dorsum, and more strongly shining; effaced traces of longitudinal striation present on metepisternal areas. Node and gaster smooth and strongly shining, virtually lacking sculpturation apart from the scattered minute pilosity-bearing punctures. Color generally as in workers, eyes black, wing veins yellowish.

♂. 6 specimens, from various Italian, French, and English localities, are identical in general structure. They have the following dimensions; HL 0.54-0.58 mm; HW (across eyes) 0.61-0.64 mm; CI 112-116; WL 1.06-1.18 mm; PNL 0.19-0.22 mm; PH 0.34-0.39 mm; DPW 0.25-0.28 mm; maximum diameter of eye 0.27-0.31 mm; ocular index 44-47. Palpal formula (4 specimens dissected); *Maxillary* 5; *Labial* 3. Wing venation as in ♀. General structure very similar to *P. pennsylvanica* (figs. 9-14). The few points of difference apart from the smaller size include the following: Genitalia in general similar, but the pygidial spine distinctly weaker; sculpturation lighter, *pennsylvanica* has a shallow, and somewhat obscure puncturation on most parts of the head and mesosoma, which dulls the reflections of these parts, while *coarctata* has the same surfaces smooth and highly polished. The color tends to be a little darker than in *pennsylvanica*.

Immature Stages: I have seen no larvae of *P. coarctata*, but it may be dependably assumed that they have 4 pairs of glutinous "doorknob" tubercles. These have been referred to in the literature on a number of occasions (e. g., Donisthorpe [1915], Escherich [1917, p. 96-97]) and a figure was published by Karawajew (1934). The pupae of all castes are enclosed in cocoons.

DISTRIBUTION. The following list includes all records of *coarctata* known to me. Most are represented in fig. 21. Material studied here is represented by closed circles on the map and unverified published records by open ones. Some of the localities listed could not be placed with available maps and atlases and are not included in fig. 21.

P. coarctata appears to have its center of distribution in the northern Mediterranean part of Europe. The records from North Africa and the Middle East are too sparse to allow a conclusion as to the abundance of the species there, or as to whether it is distributed clear across North Africa. The records from Britain, Germany, and the U. S. S. R., indicate a probable distributional limit at a latitude of about 52°N (note that the northern English records are dubious). *P. coarctata* has not been recorded from Scandinavia, although several active myrmecologists have resided there. The lack of records from some other areas (e. g., Turkey) is no doubt due to deficient collections.

EUROPE AND MIDDLE East

AUSTRIA: *Styria*: Podcetrtek (Jaeger) MCZ. *Tirol*: Localities from Mayr (1858): Hauslach; Kaiser Aue; Rodler Aue; Rungelstein; Salten; Talferbeet. **BELGIUM:** Unspecified records by Bondroit (1918) and Stitz (1939); recorded from central and north Belgium by Bondroit (1910). Localities from Bondroit (1912) and Van Boven (1947): Burnot; Hautes Fagnes; Riviere; Waulsort; Yvoir. **BRITISH ISLES:** *P. coarctata* has been listed from the following English counties by Donisthorpe (1927): *Cornwall, Devon,*

Dorset, Durham, Hampshire, Kent, Lancashire, Middlesex, Surrey, Sussex, Warwickshire, Isle of Wight. Bedfordshire and Glamorgan (South Wales) were added by Collingwood (1958). I have seen about 60 British specimens of all castes. Devon: Brixham (R. C. L. Perkins) Oxford coll.; Lannacombe, IV.1955, Widecombe, IV.1953 (C. A. Collingwood). Surrey: Box Hill (Donisthorpe) Nat. Mus. Wales coll. (C. E. Stott) Oxford coll. Kent: Charing, Chatham, Witstable (D. Chitty or R. C. L. Perkins), Oxford coll.; Dugness, Sidcup, VIII. 1959 (C. A. Collingwood). *P. coarctata* is unknown from the northern parts of Britain, or from Ireland, and has not been recorded from the Scilly or Channel Islands. The Warwickshire records (Warwick and Sutton Coldfield) date to the 1870's and have not been corroborated by more recent collections; Collingwood (1955) suspects that they were based on *Hypoponera punctatissima* specimens. The more northern records from Lancashire and Durham are possibly also questionable. BULGARIA: Unspecified record by Wesselinoff (1936). CZECHOSLOVAKIA: Records from Soudek (1931) and Kratochvil (1944): Beresasu; Brno; Byciskale; Cejč; Chuchle; Hady; Kleč; Levice; Macocha; Měcherniche; Mohelno; Moravia; Pavlovskych; Pilis; Podkarp; Pouzdrany; Putnoku; Slovensko; Straznice; Suchy; Svatojanske; Vel Mezirici; Veveri; Vrané; Vysocany; Závisti; Zleb. FRANCE: Records from Latreille (1802) and Bondroit (1918) are cited by locality only: Allier; Chartreux; Fontainebleau, VI.1955 (C. A. Collingwood); Gentilly; Le Creusot; Mesvres; Maritime Alps, V. 1953 (C. A. Collingwood); Normandy; vicinity of Paris; Yvoir. GERMANY (WEST): Records from Karawajew (1912), Stärcke (1926), Gösswald (1932), and Gösswald and Halbertstadt (1961): Bonn; Brohl; Idarwald; Rhön; Ruine Ockenfels; Sayntal; St. Goar; Weisbaden; Witterschlick; vicinity of Würzburg. GERMANY (EAST): Records from Schimmer (1908): vicinity of Leipzig-Ammelshain; Kollmburg; Osthange des Trebsener. GREECE: Kerkira: Gasturi, 2.IV.1929 (Beier) MCZ. HOLLAND: Unspecified records by Stitz (1939) and Van Boven (1959). Limburg: Exaeten; Valkenburg (Stärcke, 1926). HUNGARY: Ofen (=Buda) (Mayr 1856). IRAQ: Shaglaw, V.1952 (N. A. Weber). ITALY: Abruzzi: Chieti (Emery 1916). Apulia: Monte Gargano (Emery 1914). Calabria: Sambiasi, V.1920 (C. Menozzi) MCZ. Elba: Monte Capanne, III-IV.1921 (Moczarski-Scheerpeltz) MCZ. Emilia: Forli (Zangheri) MCZ. Records published by Consani & Zangheri (1952), at about 200-250 m: Boscodi Ladino, Dovadola, Farazzano, Fognano, Grisignano, Magliano, Pineta di Classe, Pineta di S. Vitale, Sardavilla, Virano; at 250-850 m: Bertinoro, Celle di Mercato, Fognano, Polenta, Saracene. Latium: Lazio, Lago di Albano, III.1919 (Luig) MCZ. Liguria: Belvedere (Emery 1916a) Genoa, IV. 1917 (Menozzi) MCZ; Rapallo (Forel 1895). Lombardia: Cremona, V.1923 (Baldoni) MCZ; Lavarone, VIII.1911, MCZ; Merano, VIII.1924 (Springer) MCZ. Sardinia: Sorgono, 1912, (A. H. Krausse) MCZ. Sicilia: Ragusa, MCZ. Tuscany: Arezzo (Emery 1916b), Giglio (Emery 1915), Pergine (Emery 1916a), Monte Argentario, III. 1921 (Moczarski-Scheerpeltz) MCZ. Venezia: Duino, XII.1924 (Springer) MCZ; Euganei, IX. 1920 (Moczarski-Scheerpeltz) MCZ; Giardini, IX.1934 (Gridelli) MCZ; Monte Chiampon, VIII.1920 (Springer) MCZ; Monfalcone, IV.1921 (Finzi) MCZ; San Daniele, VIII.1920, MCZ; San Pietro del Carso, IV.1933 (Springer) MCZ; Timavo (=Recca) III. 1936 (Schatzmeyer) MCZ. LEBANON: Hadreth Cedars, 1700 m, 18-20.VII.1953 (K. Christiansen) MCZ. LUXEMBOURG: Records by Latreille (1802) and Stumper (1953). ROUMANIA: Records from Montadon and Santschi (1910): Bucarest; Comana Vlasca; Moldavia; Vallée du Berlad. SYRIA: Latakia, 800 m, oak grove leaf litter, 2.VII.1953 (K. Christiansen) MCZ. SOVIET UNION: Records from Mayr (1859), Arnoldi (1932)

and Karawajew (1934): *Armenian S. S. R.*: Dolizhan; Yerevan. *Azerbaydzhan S. S. R.*: Elisavetpol (=Kirovbad), Lenkoran, Podgornoye. *Georgian S. S. R.*: Batumi, Tsichis-Tsiri. *R. S. F. S. R.*: Abrau, Anapa, Belaja, Durso, Ilskaja, Kizlyar, Krasnodar, Niederlauf, Kutais, Niederterek, Ozereika. *Ukraine S. S. R.*: Don Biological Station at Zmiyev near Khar'kov Gadyach, Kiyev, Luk' janiuka, Gurzuf, Kerch, Nikita, Sevastopol, Simferopol, Yalta, Zvenigorod region — Okolitz and Murzintzi. *SPAIN*: *Balaeres*: Majorca, Palma (Bernard 1956). *Catalonia*: Centellas (Menozzi 1922). *Santander*: Jesus de Montes (H. Franz) Collingwood coll. *Sevilla*: Seville (Forel 1895). *Valencia*: Benicarlo (H. Franz) Collingwood coll. *SWITZERLAND*: Records from Forel (1874), are cited by locality only: Argovie; Geneva; Graeffe; Lorenzbad; Monte Centri, Bironico, VII.1907 (W. M. Wheeler) USNM; Sion; Vaux; Zurich. *TRIESTE*: Basovizza, 12.V.1931, MCZ; Boschetto, 12.IV.1920, MCZ; Zaule, II.1921 (B. Finzi), 19.IV.1929, (Springer) MCZ. *YUGOSLAVIA*: *Dalmatia*: Dubrovnik, Split (Zimmerman 1934); Mt. Lisina, IX.1938 (Springer) MCZ; Sibenik (Weirather) MCZ; Sucurac, various dates 1912-1922 (Novak) MCZ; Zemonica, VIII-IX. 1914 (Novak) MCZ. *Istria*: Abbazia, XII.1924 (Springer) MCZ; Levade, 1923 (Ravasini) MCZ; Monte Tiarno, V.1923 (Springer) MCZ; Porta Porton, 19.IV.1933 (Springer) MCZ; Rovigno, IV.1926 (Springer) MCZ; Salyore, IV.1922 (Finzi) MCZ. *Hercegovina*: between Zelenika and Kameno (Zimmerman 1934).

NORTH AFRICA

ALGERIA: Edough (Emery 1916c), La Verduze (Emery 1891), St Charles (Santschi, 1921). *MOROCCO*: Mamora forest (Bernard 1945). *TUNISIA*: Cap de la Sante (Dr Normand) Santschi coll., El Kef (Dr Normand) Santschi coll., Ain Draham, Sousse (Santschi 1921).

ECOLOGY. Little detailed published information is available concerning this subject apart from Gösswald's (1932) review of his collections from the vicinity of Würzburg, Germany. He gives records for 20 nests, one of which was taken in sand, in the foundations of a house; with 19 in limestone (Haupmuschelkalk) soils. More colonies (15) were taken on upper Haupmuschelkalk soils than on those of the middle (3) or upper (1) parts of the formation; no possible explanation for this apparent correlation was suggested. Gösswald noted preference by *coarctata* for dry stony soils, but observed no clear correlation between vegetation type and distribution of the ant. Specimens were collected in woods, woods margins, a domestic garden and in dry grassy wasteland; the species was found most commonly in the latter habitat. Eighteen nests were located under stones, and two were in the soil without a covering object; no general structural regularity of the nests was noted, but it was suggested that the galleries must penetrate deeply into the soil. The largest colony contained 30 workers.

Gösswald gave September as the flight season in Germany, and noted that pupal cocoons containing alate females were found in nests during August. In Britain, Donisthorpe (1927) gives records of free flying alates taken from late August (28th) to late September. I have seen a single male from Charing, Kent, collected on 24.VIII.1904; otherwise all alate specimens agree with Donisthorpe's data. Four Italian and Yugoslavian males in the Finzi collection (MCZ) bear the month only — August in all cases.

2. *Ponera atavia* Mayr

Ponera atavia Mayr, 1868, Beitr. Naturk. Preuss. **1**: 72, Taf. IV, figs. 66-69, ♀, ♂, original description.—Wheeler, 1914, Schr. phys.-ökon. Ges. Königsberg **55**: 38, fig. 9, a-c, worker.

This Baltic Amber species is apparently allied to *P. coarctata*.

The *atavia* material studied by Mayr and Wheeler was presumably lost, with the rest of the Königsberg Geological Institute collection, during World War II. There are no specimens in the MCZ Amber collection, and presumably none now exist, there or elsewhere. Both earlier authors illustrated the castes they described; so some features of *atavia* can be established. This is not the case with the other Baltic Amber *Ponera* species, *P. gracilicornis* Mayr, which I consider to be a member of tribe Ponerini, but of uncertain genus (Taylor 1964). Mayr also described a *Ponera succinea* from the Baltic Amber; this species is clearly best referred to *Trachymesopus* (Wheeler 1914).

The figures of Mayr and Wheeler allow verification of the generic placement of *atavia*, and in general support its affinity with *coarctata*. The following characters are significant: In the worker, the general form of the head and mesosoma, and especially of the propodeum and petiolar node; the mandibular dentition, the reduced eyes, and the general structure of the tibial spurs; clypeus and the antennae. The wing venation of the alates must also be considered along with the absence of an anal lobe in the hind wing of both sexes, and the presence of a terminal pygidial spine in the male.

The habitus of the worker, as illustrated by Wheeler, is close to that of *coarctata*. He noted the following characters distinguishing the 2 species:

1. Head relatively shorter in *atavia*, with eyes placed further forward.
2. Basal joint of antennal funiculus longer in *atavia* than in *coarctata*.
3. Mesonotum differently shaped.
4. In *atavia* the propodeum is longer, and sub-marginate on sides of its basal face as well as on those of declivitous one.

Mayr noted that the males differed from those of *coarctata* in possessing Mayrian furrows on the mesonotum.

Considering the peculiar zoogeographic affinities of the *coarctata* group, and its relative distinctiveness from the Indo-Australian *Ponera* species, it is unfortunate that further material of *atavia* is not available. All that can be said is that this species seems to be a good *Ponera*, and superficially resembles the living *coarctata* group species. Further details of its relationships with these forms and with the Indo-Australian members of the genus, especially with such forms of the Japanese *P. japonica*, are not available.

3. *Ponera pennsylvanica* Buckley Figs. 1-3, 5, 9-14, 18-20, 22.

Ponera pennsylvanica Buckley, 1866, Proc. Ent. Soc. Phila. **6**: 171, worker. Type locality: Philadelphia, Pennsylvania.

Ponera coarctata subsp. *pennsylvanica*: Emery 1895, Zool. Jahrb. Syst. **8**: 287, worker, ♀, ♂.—Wheeler, 1900, Biol. Bull. Woods Hole **2**: 44, figs. 1-4, worker, ♀, ♂.—M. R. Smith, 1936, Ann. Ent. Soc. Amer. **29**: 426, worker, ♀; 1947, Amer. Midl. Nat. **37** (3): 538, plate 4, fig. 14, worker.—Creighton, 1950, Bull. Mus. Comp. Zool. Harv. **104**: 48.

Ponera contracta: Provancher, 1889, Faune Entomologie Du Canada 2, Hyménoptères (Additions et Corrections): 242, worker, gyne, ♂.

TYPES. No types are known to exist. This species is unlikely to be confused with any other, and usage of the name has been unambiguous; I have not, therefore, designated a neotype.

DIAGNOSIS. A member of the *P. coarctata* species group, endemic to eastern North America. Distinguished from other species of the genus, including *coarctata*, by the characters given under the latter. The larger size, presence of a distinct dorsal mesometanotal suture in the worker, and the undifferentiated antennal club in the female castes, distinguish *pennsylvanica* from *P. exotica* M. R. Smith, the only other known New World species of *Ponera*. *Exotica* is evidently not closely related to *pennsylvanica*, and is likely introduced from the Indo-Australian area, though it is not yet known from there.

Among the various ants listed previously as subspecies of *P. coarctata* this is the only one congeneric with it; all others belong in *Hypoponera*. The describer, Buckley, did not indicate the relationship between this species and *coarctata*, but Emery (1895) reduced *pennsylvanica* to a subspecies of the latter. It has maintained this status consistently since that time. In spite of the taxonomic difficulties inherent in the allopatry of these forms, their separate specific status seems certain. The fact that earlier authors have not recognized the two as good species apparently does not reflect personal opinion, but merely that none of my predecessors have critically considered their relative status.

Worker: There is no significant geographical variation in the standard dimensions and indices. Fifty-three specimens from all parts of the range (no more than 3 from a single locality), gave the following values: HL 0.64–0.76 mm; HW 0.53–0.63 mm; SL 0.45–0.55 mm; CI 77–85; SI 83–90; PNL 0.20–0.25 mm; PH 0.42–0.50 mm; DPW 0.27–0.40 mm; PNI 70–84. General features as in figs. 18–20. Close to *P. coarctata* in details of mandibular dentition, clypeal structure, palpal formula, size and position of eyes, and general post-cephalic structure. Profile of mesosomal dorsum more plane—not impressed at mesometanotal suture. Propodeum and node in dorsal view more robust than in similar size *coarctata* specimens. Subpetiolar structure almost identical.

Sculpturation much more distinctly developed than in *coarctata*. Head opaque, coarsely and closely punctate, with virtually no interpunctural surfaces remaining. Scapes opaque, finely shagreened. Dorsum of mesosoma subopaque, closely punctate, about as on the frons of *coarctata*. Sides of mesosoma slightly less densely punctate than dorsum, subopaque, with propodeal sides feebly shining and a little less heavily punctate than remainder. Slight traces of longitudinal striation present on metepisternal area. Node and gaster much as in *coarctata*, almost imperceptibly more densely punctate. Pilosity and pubescence as described for *coarctata*. Color similar, but with a slightly more reddish hue.

Workers of *P. pennsylvanica* are remarkably uniform in size, coloration, sculpturation and pilosity throughout the distributional range of the species. Most samples include some relatively light colored specimens, probably indicating that the callow period is prolonged. There is marked intrademe and intranidal variation among the workers, based on allometric characters. Head length and scape length are negatively allometric relative to HW (k = about 1.40–1.45). Hence small individuals tend to have lower cephalic index values ($HW \times 100 / HL$) and higher scape index values than do large ones. Pronotum width

and petiole height are approximately isometric relative to HW, and dorsal petiole width is positively allometric relative to HW ($k=ca. 0.7$). As HW and pronotum width are isometric, small specimens tend to yield lower values for petiolar node index (Dorsal petiole width $\times 100$)/PW than do larger ones. Several colony series have been checked to verify that this type of allometry is found intranidally, and comparison of the Canadian specimens and those from the District of Columbia shows that the allometric relationships are not significantly different in the two areas. There is a slight tendency for small specimens to be less densely sculptured than large members of the same sample, but otherwise there is little general variation (cf. with *P. coarctata* above and *P. leae* below).

♀. (figs. 1-4, 5). 17♀♀ from all parts of the distributional range have the following measurements: HL 0.37-0.41 mm; HW 0.30-0.35 mm; SL 0.24-0.29 mm; CI 82-86; SI 80-84; PW 0.27-0.31 mm; PNL 0.12-0.15 mm; PH 0.28-0.31 mm; DPW 0.22-0.25 mm; PNI 76-80; maximum diameter of compound eye 0.09-0.11 mm; ocular index 27-31. Palpal formula (2 specimens dissected): *Maxillary* 2: *Labial* 2, as in the worker. Wing venation as in *P. coarctata*. Differing from the workers in the usual characters of full sexuality. Similar in general to *P. coarctata*, but larger in size. There is no overlap in the ranges for PW, PH, DPW, SI and PNI in ♀♀ of these 2 species. The petiolar node is distinctly broader in *pennsylvanica* (compare the PNI values), and thinner when viewed from above (cf. figs. 3 and 4). The sculpturation is much more heavily developed than in ♀♀ of *coarctata*; the diagnostically important sculptural characters being: mandibles, clypeus, frons, and scapes as in worker. Entire mesosoma opaque, with a close cover of punctures about 0.01 mm in diameter. Node and gaster feebly shining, with a finer more scattered puncturation than mesosoma—the punctae of the disc of the first gastric segment, for example, about 0.007 mm in diameter, separated by distances about equal to 1.5 to 2.5 \times their maximum diameter. Color as in worker.

♂. (figs. 9-14). Details of the ♂ anatomy of *P. pennsylvanica* are given above under the generic diagnosis and features distinguishing ♂♂ from those of *P. coarctata* are cited under the latter. The following notes are based on 20 specimens from all parts of the species range: HL 0.60-0.63 mm; HW (across eyes) 0.64-0.70 mm; CI 107-113; WL 1.04-1.22 mm; PNL 0.20-0.23 mm; PH. 0.35-0.41 mm; DPW 0.28-0.31 mm; maximum diameter of eye 0.27-0.32 mm; ocular index 43-46; palpal formula (6 specimens dissected): *Maxillary* 5: *Labial* 3, as in *P. coarctata*. Wing venation as in ♀. Color medium to rather dark brown; eyes black; clypeus, mandibles, legs and gastric apex lightly infuscated; wing veins yellowish.

Immature Stages: The larva of *P. pennsylvanica*, like that of *P. coarctata* has 4 pairs of dorsal abdominal "mushroom" tubercles. A detailed description with figures has been published by G. C. & J. Wheeler (1952). The pupae of all castes are enclosed in cocoons.

MATERIAL EXAMINED AND PUBLISHED RECORDS. In the following list all previously published records are listed, and all material seen during this study is indicated. Standard abbreviations for source collections are used. The following collectors are cited by their initials: W. L. Brown, W. M. Mann, C. D. F. Miller, M. R. Smith, R. W. Taylor, W. M. Wheeler, E. O. Wilson; the name of the collector W. M. is not known.

CANADA: I have seen all Canadian material listed here: *Nova Scotia*: Digby (J. Russell) AMNH, USNM, MCZ. *Ontario*: (Unless otherwise indicated all records are based on specimens from the collections of CDA, Ottawa). Arnprior, VII.1914 (C. MacNamara).

Bell Corners, colony with callow workers, pupal and imaginal ♂♂, 9.IX.1952 (CDFM). Chatterton, 29.VI.1960 (G. L. Ayre) CDA-Bellvue coll. Eldorado, Hastings Co., ♂, 27.IX.1904 (Evans). Galesburg, workers under bark, 19-20.IV.1910 (T. Tanquary). Georgetown, 2.III.1894; ♂♂, 31.VIII.1893. Glen Ross, Hastings Co., 10.V.1902 (Evans). Highlands, 13.V.1957 (WM); 940 m, 12.V.1957 (WM). Jordan, VI.1915 (G. H. Curran); 24.V.1916 (W. A. Ross); ♂, 12.IX.1917 (W. A. Ross). Leamington, 29.V.1937 (G. S. Walley). Marmora, colony under stone, pasture, 2.VI.1952 (J. R. Vockeroth); colony with alate ♀♀, 13.VIII.1952 (CDFM). Normandale, 2.VII.1956 (CDFM). Ottawa, no further data, 22.XI.1912. Pentanguishene, ex soil, 25.IV.1933 (R. J. Reye) USNM. Pt Pelee, 8.VII.1931 (M. Talbot) AMNH. Trenton, ♂♂, 13.IX.1903 (Evans). *Quebec*: Aylmer, Queens Park, male, 15.IX.1924 (A. R. Graham). Dorval, 20.IV.1915 (J. H. Beulne). Hull, dealate ♀, 14.VIII.1897. King Mountain, Old Chelsea, 330 m, colony among dead leaves on grassy ground, 27.VIII.1959 (J. R. Vockeroth). Montreal, 16.V.1915 (J. I. Beulne) CDA, USNM. Old Chelsea, colony with imaginal and pupal ♂♂, and ♀♀, 9.IX.1952 (CDFM). Quebec, ♂ and ♀, 15.XII.1962 (A. Francoer). Wakefield, workers ex Berlese funnel sample, lichens, 2.V.1954 (E. C. Becker).

UNITED STATES: Unless otherwise stated all records are based on specimens in the MCZ collection. *Alabama*: Dale Co., Arton, 20.IV.1949 (EOW). Tuscaloosa Co., Duncanville, 21.II.1949 (EOW); Peterson, 10.VIII.1947 (EOW). *Arkansas*: Washington Co., ex soil, orchard, 25.III.1938. *Colorado*: Loveland, 7.VIII.1957 (M. Sliffe) CDA. Localities from Gregg (1963): Beecher Island, 1080 m. Boulder area-Bear Canyon, 1830 m. Gregory Canyon, 1730 m. Mesa Verde National Park, 2100 m. *Connecticut*: Unspecified record by Wheeler (1906). Caanan, ♂, 29.VIII.1952 (A. Stone) USNM. Colebrook, colony with alate ♀♀ and ♂♂, 20.VIII.1900 (WMW) MCZ, AMNH; dealate ♀, 24.VIII.1901 (WMW) AMNH; 21.VII.1905 (H. L. Viereck) USNM. *Delaware*: Christiana, tree hole berlesate, 31.V.1953 (R. S. Howard); Wilmington, heavy oak-maple woods, 18.IV.1953 (R. S. Howard). *District of Columbia*: Unspecified record by Emery (1895). Specimens with no further data, collected in 1884, 1885 and 1887 (T. Pergande) USNM. Shaw Pond, alate ♀, 14.XI.1926 (H. S. Barker) USNM; Washington, dealate ♀, 11.III.1894 (F. C. Pratt). *Florida*: Unspecified records by Emery (1895). Gainesville; Monticello, (WMW 1932; MRS 1936). *Georgia*: Atlanta (MRS 1936). Burton; Spring Creek; Thalman (WMW 1913; MRS 1936). *Idaho*: Twin Falls, 1933 (A. C. Cole). *Illinois*: Unspecified records by Forel (1899). Records here by locality only after MRS (1936) or Gregg (1944)—some Smith records have been verified: Algonquin; Bloomington; Carte Woods; Centralia; Charleston. Chicago region, various localities (Talbot 1934; Gregg 1944); Danville; Galena; Giant City State Park, mesic hardwood forest, 13.VIII.1958 (WLB); Gorham, Fountain Bluff, forest debris, 6.IX.1956 (Smith & Stannard); Hadley; Harrisburg; Herod; Hodgkins; Lagrange; Little Grassy Lake, near Carbondale, VIII.1958 (WLB); Makanda; New Lenox; Nominee; Norman; Orlando Park; Palos Park; Rockford (WMW) AMNH; Savoy; Trelease Woods, near Urbana, 8.VIII.1958 (WLB); Urbana; Volvo; Wankegan; White Heath, 11.IX.1939 (J. C. Dirks) USNM; Zeigler. *Indiana*: Records after WMW (1916), MRS (1936), and Gregg (1944) cited by locality only: Brown County State Park, 22.VIII.1958 (WLB); Chesterton; Grand Chain; Smith; Starke County; Wyandotte (W. Blatchley) AMNH. *Iowa*: Records from Buren (1944), and MRS (1936) are cited by locality only: Ames; Clinton; Inwood; Muscatine; Oak Grove State Park; Sabula; Stanhope; Sioux City, 18.V.1931 (G. N. Ainslie) AMNH. *Kansas*: Herrington, IV.1918 (J. R. Horton)

USNM. Isage City (A. C. Burrill); Riley Co., 20.III. (J. B. Norton) USNM. *Kentucky*: Ashland (MRS 1936). Louisville, 25.VIII.1946; dealate ♀, 1.IX.1950; colony with alate ♀♀ and ♂♂, 1.XII.1946 (EOW). Vanceburg (MRS 1936). *Louisiana*: Tallulah (MRS 1936). *Maine*: Records from WMW (1908), MRS (1936) and Wing (1939) cited by locality only: Bar Harbor; Casco Bay; Enfield; Lincolnville, alate ♀ and ♂, 23.VIII.1926 (E. B. Bryant); Oakland; Old Town; Orono; Sebago Lake, 2-10.VIII.1921 (G. E. Wheeler) G. E. Wheeler coll. *Maryland*: Unspecified record by Emery (1895). Plummer's Island, 12.IV.1908 (E. A. Schwarz); 20.III.1910 (J. G. Crawford); 23.IV.1923 (H. S. Barber) all USNM. *Massachusetts*: Arlington, colony with alate ♀♀ and ♂♂, 30.VIII.1952 (EOW); Blue Hills, Canton, 5.IV.1953 (EOW); Brewster (Sturtevant 1931); Cambridge, nest under stone, suburban woodlot, IX.1961 (RWT); Chestnut Hill, IV.1930 (WMW) USNM; East Falmouth (Sturtevant 1931); Ellisville, IV.1910 (WMW) MCZ, AMNH; Holliston, alate ♀, 13.IX. (N. Banks); Mt Tom (C. Dimmock); Woods Hole (WMW 1906). *Michigan*: Ann Arbor, 5.VII.1948 (G. C. Wheeler); Charity Island (MRS 1936). Cheboggan Co., worker under bark, moist sand, deep woods in gorge, 16. VII.1944 (M. Talbot) Talbot coll; Michigan Biological Station, ex rotten log, larvae and queen pupae, 8.VII.1945 (M. Talbot) Talbot coll. Detroit (H. J. Hubbard). Lakeside (Gregg 1944). Livingston Co., Edwin S. George Reserve (Talbot 1953). Porcupine Mountains (O. McCreary) AMNH. Roscommon Co., Ogemaw State Game Refuge, nest in lichen covered sandy mound, 17.VII.1939 (M. Talbot) Talbot coll. Warrens Woods, near Lakeside, ex leafmold, Beech tree hole, 27.IX.1953 (O. Park). *Minnesota*: Saganaga Lake (Gregg 1946). *Mississippi*: Unspecified record by Emery (1895). Corinth; State College; Lucedale (MRS 1936); 2 km S of Wiggins, 27.VI.1950 (K. Christiansen). *Missouri*: Columbia (MRS 1936); De Soto, ex log mold, 17.VIII.1953 (G. W. Myers). St. Charles Co. (Talbot 1957); Sullivan, 16.X.1954 (M. Pickard) USNM. *Nebraska* Lincoln; Warsaw (MRS 1936). *New Hampshire*: Contoocook (MRS 1936); Franconia (A. T. Slosson) AMNH; Monadnock Mt, lower E slope, 26.IV.1954 (WLB). *New Jersey*: Unspecified records by Emery (1895) and Wheeler (1905). Bridgetown, 31.VII.1954 (WLB); Camden (MRS 1936); Fort Lee Distr., 26.VII.1904, AMNH; Glassboro, 4.VII.1898, AMNH; Great Notch (WMW) AMNH; Halifax (MRS 1936); Hunterdon Co., IV.1916 (WMW); Lakehurst (MRS 1936); Newfoundland (WMW); Pomona, 31.VIII.1954 (R. Freund). *New Mexico*: Las Vegas hot springs, III.1903 (Mrs Cockerill) AMNH. *New York*: Bronxville, IX and 11.VII.1904 (WMW) AMNH; Cold Spring Harbor (WMW) AMNH; Chatham, ♂, 30.VIII.1904 (A. P. Morse); Freeville, ♂, 1.IX.1922; Ithaca (Chittender) USNM; Jamestown (MRS 1936); New York City (C. T. Brues) AMNH; Riverhead, ♂, 18.IX. 1913; Sea Cliff (N. Banks); Staten I., numerous localities (Davis & Bequaert 1922); Syracuse (MRS 1936); Tuxedo, 20.IX.1926 (W. S. Creighton); West Farms, N. Y. City (J. Angus) AMNH; White Plains, 18.VI.1905 (WMW) AMNH. *North Carolina*: This species is widespread in North Carolina, in all regions—Mountain, Piedmont Plateau, and Coastal Plain as shown by W. G. Carter (1962a, 1962b). The numerous records cited by Carter are not repeated here, others are: Ashville (N. P. Jacot); Black Mts, 24.V.1904 (WMW); Bat Cave; Blue Ridge; Buncombe Co.; Craggy (WMW, 1904); Chapel Hill, 22. VIII.1938 (G. C. & J. Wheeler); Cherokee, 600 m, Berlese funnel sample, workers and dealate ♀♀, 29.V.1957 (W. R. M. Mason) CDA; Duke Forest, 14.VII.1933 (A. S. Pearse); Grey Beard Mt, 26.V.1904, AMNH; Henderson (Wheeler 1904); Lake Taxaway (A. T. Slossom); Santeetlah Lake Dam, 22.VI.1950 (K. Christiansen); Sugar Fork (WMW 1904); Swannanoa

Valley, 21.V.1904, AMNH: *North Dakota*: Two records at the far west of the state were recently published by G. C. & J. Wheeler (1963): Mckenzie Co., virgin prairie near Yellowstone River (GCW No. 31-149-104); Slope Co., near Little Missouri River, open *Pinus ponderosa* woods (GCW No. 9-136-104). *Ohio*: Unspecified record by the Wessons (1940). Ashtabula Co., common, nesting in rotting stumps or logs, under stones, in acorns, alates between 15.VIII. and 8.X (Headley 1943); Columbus (G. H. Kennedy) USNM; Killdeer Plain area (Amstutz 1943); Put-in Bay (MRS 1936); Seneca Co., (Headley 1952); Wayne Co., Funk's Hollow, 5.X.1962 (A. MacDougall); Willard, 22.VIII.1931 (M. Talbot) MCZ, AMNH. *Oklahoma*: McCurtain Co., several records from Berlese funnel samples of litter on or near rotten stumps, VIII.1962 (W. G. Carter); Payne Co., 7 records from berlesates of leaf litter, usually near rotten stumps, VII-VIII.1962 (W. G. Carter). *Pennsylvania*: Unspecified record by Emery (1895). Highspire, 28.III.1908 (W. S. Fisher) USNM. Linglestown, 9.IV.1909 (R. P. Meyers). Philadelphia, 2.IV.1899 (J. F. McClandon). Poconos, Keipel Mt, peat bog near U. S. 611, 23.IV.1947 (WLB). Rockville, 12.IV.1908 (P. R. Myers) USNM. Tinicum I., 3.IV.1897, USNM; 4.IV.1909 (G. M. Greene). *South Carolina*: Clemson College (MRS 1936); Clemson, dealate ♀, ex flood debris, 30.III.1944 (O. L. Cartwright). *South Dakota*: Canton (MRS 1936). *Tennessee*: Records from Cole (1940), Dennis (1938) and Smith (1936): Chuckey; Knoxville; Great Smoky Mts.-Cove Mt; Greenbriar Cove, 550 m; Greenbriar Pinnacle, 970 m; Ramsay Cascade, 1275 m; Circle Cove near Gatlinburg; Greeneville; Middleton; Morristown; Mosheim; Parsons; Ripley; Slabtown; Tusculum College. *Vermont*: Unspecified record by Wheeler (1906b). Lyndon (WMW) MCZ. *Virginia*: Unspecified record by Emery (1895). Specimens with no further data, collected in 1883, 1884, and 1887 (T. Pergande) USNM. Black Pond, Fairfax Co., (WMM) USNM. Chain Bridge (WMM) USNM. Falls Church, 10.VII-18.X; alates on 5. VIII, 5, 8, 26.IX. (N. Banks); 30.I.1944 (F. André) USNM. Hog I., 1928 (WMM) USNM. Konnarock, VIII.1936 (WMM) USNM. Lexington; Mountain Lake (Cole 1949). Mt. Shenandoah, base of Short Mt., 6.VI.1941 (A. B. Gurney) USNM. Thoroughfare Gap (J. C. Bridwell) USNM. *West Virginia*: Morgantown (MRS 1936). *Wisconsin*: Unspecified records by Forel (1899). Baraboo (Burrill & Smith 1918); Delavan, 27.IV.1912 (A. C. Burrill); Madison (MRS 1936); Milwaukee (G. E. Brown) AMNH.

DISTRIBUTION AND ECOLOGY (fig. 22). The known distribution of *pennsylvanica* includes the eastern United States and Canada, from Quebec south to the Gulf Coast, and west to about the 97th meridian. This range corresponds remarkably well with the area carrying the Eastern Deciduous Forest Formation. The western and southern extensions of which are indicated on the map (see also Braun 1950); the western limit of the forest formation proper is shown as a dotted line; that of the forest-prairie transition belt as a solid line. Tongues of transition forest extend westwards into prairie grassland carrying with them forest pockets in which *pennsylvanica* occurs. The area of forest or transition country from which *pennsylvanica* has been recorded is shaded on the map; apparently this is the main range of the species. The few records known from outside the forest zones are indicated as dots.

The records appear to indicate a northwestern limit at about the latitude of northern Iowa. However, there are more northerly records from Saganaga Lake in extreme NE Minnesota (Gregg 1946), and from the Porcupine Mts in the upper peninsula of Michigan. These must be close to the limits of the range in this area.

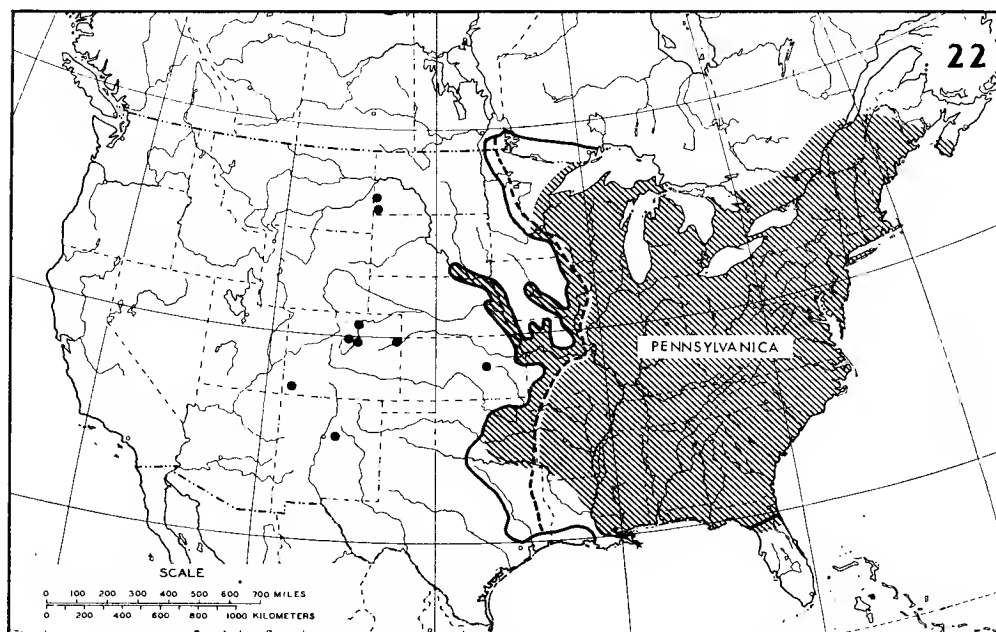


Fig. 22. *Ponera pennsylvanica* Buckley, Distribution (see text for explanation).

Further east, in the southern Great Lakes area and New England, *pennsylvanica* seems fairly common at latitudes where it is reportedly rare in the west. The northernmost known records are from the vicinity of Quebec. The Digby, Nova Scotia, record may indicate present distribution at least as far as the "neck" of that province, however, the species is unknown from northern Maine and New Brunswick. *P. pennsylvanica* may be taken at low elevations in northern New England, but it is less common there than in the southern part of the area. Sturtevant (1931) noted that it was much less common on Cape Cod than near New York City.

The northern distributional limits are almost certainly set by deteriorating climatic conditions, and in fact correspond fairly well with the 40° Fahrenheit (4.5°C) mean annual temperature isotherm (see Vischer 1954: map 3). *Pennsylvanica* apparently declines in abundance northwards, from a line running approximately through Milwaukee and Ottawa, on the map projection used in fig. 22. This corresponds almost exactly with the 45° Fahrenheit (7.4°C) mean annual isotherm as shown by Vischer. Ignoring the two extreme northwestern records, the main northern limit of *pennsylvanica* trends southwards as it moves inland towards the central plains. This trend is perhaps correlated with the increase in severity of climate at a given latitude moving westwards across the Great Lakes area.

The western limit of the main distributional range is clearly marked. All records available from South Dakota, Nebraska, Kansas, and Oklahoma, being towards their eastern areas; with the extreme western ones falling almost exactly in a north-south line. Details of the distribution in these States and in Iowa are interesting, for most records fall within the area of the Eastern Deciduous Forest Formation or its prairie-transition belt. The Iowa records of Smith and Buren are significant in this connection. This state is occupied

mainly by country floristically part of the midwestern grassland-prairie association. Two areas are within the range of the forest-prairie transition belt, as shown in fig. 22: (1) the valleys of the Mississippi and Des Moines Rivers and (2) the drainage system of the Missouri River, which forms a long tongue extending northwards from Missouri, along the western Iowa border. All of the Iowa records listed above fall within the transitional forest zones, and not in the prairie zones. The single South Dakota record is also from transition country, and was made in the relatively small extension of the Missouri River valley "transition forest tongue in the extreme south east of the state. The Nebraska records, too, both lie within the limits of this transition forest extension, at the extreme east of the state. The only known Kansas records are from Riley and Dickinson Counties, which lie outside the broad limits of the forest transition belt; unfortunately no ecological details are available.

All Oklahoma records are from the east of the state, in transition country. Professor W. G. Carter, the collector, has provided more precise ecological details than are usually available. The Payne County specimens were taken in mesic forests of oaks and other hardwoods, growing in stream floodplains and deep ravines. The area in general is characterized by large tracts of tall or mixed grassland and there are also xeric scrub oak forests in certain highland areas. McCurtain County records were also from similar mesic ravine forest in primarily grassland areas. Professor Carter (*in litt.*) recently found *pennsylvanica* common in eastern Oklahoma.

South of Oklahoma the known distributional limit has a strong easterly trend. Records from this area are scarce, but, it is notable that the 50% line of soil moisture saturation, as mapped by Vischer (1954: map 954, p. 359), follows about the same path. Considering that soil moisture values depend on interaction of numerous ecological parameters this may be significant, especially as *pennsylvanica* is soil inhabiting.

In Florida *pennsylvanica* is known only from Gainesville, in the north. It was not taken by Van Pelt (1956) in his careful survey of Welaka Reserve, slightly further south. The apparent southern limit indicated by these data almost exactly coincides with the limit of deciduous forest, and lies across an area where "one after another of the deciduous (forest) species reaches the southern limits of its range" (Braun 1950) exact limiting factors acting here on *pennsylvanica* are not clear, but considering its decline southward in Mississippi (M. R. Smith 1956) and possibly in other Gulf Coast states and Georgia (*teste* E. O. Wilson), climatic factors are probably involved. The possibility of competitive exclusion by other ant species should be considered.

In general the marginal limiting factors for *P. pennsylvanica* appear to be "density independent" ones—climatic deterioration in the north, decreasing humidity in the west and southwest, and high temperature (and humidity?) in the south and southeast. These factors seem to be effective even in areas where suitable forest occurs, such as the northwest and southwest of its range.

Although the main limits of *P. pennsylvanica* are approximately co-extensive with those of the Eastern Deciduous Forests, the ant ranges far to the west, where it is obviously very scarce (see fig. 22). As Gregg (1963) has noted, it might be expected to occur sporadically in river valley forests throughout the central plains area.

P. pennsylvanica is characteristically found nesting in deciduous forests of various types, although it may penetrate more open habitats or coniferous forests. In the Chicago region

Talbot (1934), and Gregg (1944) have reported it from stands of Black, Red, or White Oak, and mixed oak forest on sandy soil and from mixed oak forest on clay. The greatest number of colonies were found in such situations, but the species was often taken at woods margins, in fields, or along roadsides. Dennis (1938) found *pennsylvanica* widespread and common in Tennessee, in oak-pine and oak-chestnut forests over a wide elevational range (90 to 1515 m). It was found to be the most abundant of 15 species nesting in locust woods in Seneca County, Ohio, by Headley (1952). This author sampled the ants nesting in 15 square-meter plots during August 1958, and in 12 adjacent, similar sized plots in June, July and September 1949. In all 299 ant colonies were taken in the 27 square meters thus studied, with *P. pennsylvanica* by far the most common species, with 109 (36%) of the colonies collected. The next most abundant species (*Stenamma brevicorne* Mayr) had only 35 nests (12% of the total). *P. pennsylvanica* has been listed as one of the most common ants in North Carolina by Carter (1962b). He found it especially abundant on the Piedmont Plateau in various forest associations, most notably in upland mature pine and oakhickory climax stands; the elevational range being 600 to 1030 m. *P. pennsylvanica* was stated by Carter to be "predictable" in coastal forest, but scarcer than on the Plateau. All of his records, except one, were from well shaded mesic forests. The extreme northwest record from Saganaga Lake, Minnesota, was made in coniferous forest (Gregg 1946).

Nests in forest areas are usually constructed in and under rotting logs, or in rotting stumps, at all but the earliest stages of decay (Talbot 1934); in small fragments of wood, acorns or other such objects; or in soil or leafmold. In drier habitats, especially non-forested areas, the colonies are usually found in soil under stones or other material, and at times the species may be common under stones in pastures (Gregg 1944). Workers forage in or on the surface of the ground, and may be readily collected using the Berlese funnel. Headley (1952) has given details concerning nest depth and proportions, and the size and proportion of colonies. He found 217 workers in 86 nests, undoubtedly a low count. During his August 1948, Ohio, survey he found no eggs and few larvae in 86 colonies. Pupae were, however, fairly abundant, with a mean of 11.2 per nest. The largest colony contained 36 pupae of all castes, one included 15 workers and 18 pupae, 10 of which were alates. The species apparently does not overwinter any brood (Talbot 1957).

Twenty-two sexual imagos were present in 4 of Headley's August colonies, but no flights were observed by him. Mating flight activity may extend from mid-August to early October, according to dates on the specimens I have seen, and those published by Headley (1943), Gregg (1944), and Kanno (1959). Colony foundation is independent and non-claustral (Kanno *loc. cit.*), and dealate females may be taken in rotting wood, soil, moss, or curled leaves. Some very incomplete mating flight observations are given by Haskins and Enzmann (1938).

RELATIONSHIPS. The relationship between this species and *P. coarctata* has been repeatedly emphasized. The two forms are closely similar and almost certainly cognate. It is difficult to estimate which of the pair is most likely to resemble the presumed ancestral stock. The *coarctata* group is probably an offshoot from Indo-Australian stock of about the same grade as the *sinensis* and *taipingensis* groups. Its origins are probably close to those of the *P. japonica* group, and indeed *japonica* itself is the most similar of the eastern species. Unfortunately the details of male and larval structure are not available for *japonica*. [Teranishi's (1940) determination of larval specimens may be doubtful, since Japanese

authors have confused this species with *P. scabra* Wheeler.] However, the related *P. incerta* has 3 pairs of glutinous larval tubercles, and a male palpal formula of *Maxillary 4: Labial 2*. The extra fourth pair of tubercles present in larvae of the *coarctata* group appear, at present, to set them off from all other *Ponera* species. These structures are considered to represent a secondarily developed character, not a primitive one, in my view of the evolutionary relationships within *Ponera*.

B. INDO-AUSTRALIAN SPECIES

4. *Ponera alpha* Taylor, new species Figs. 23, 24, 36.

DIAGNOSIS. A New Guinean species not referable to any species group recognized below. The workers are distinguished by the following characters:

1. Size exceptionally large; head width 0.76-0.85 mm. The next largest species of *Ponera* has a maximum HW of 0.73 mm.

2. Head broad (cephalic index 88-93), with distinct median clypeal tooth, and relatively small eyes with 6 or 7 very indistinct facets. The antennal scapes exceed the median occipital border by 1-1.5 \times their maximum thickness and no antennal club is differentiated.

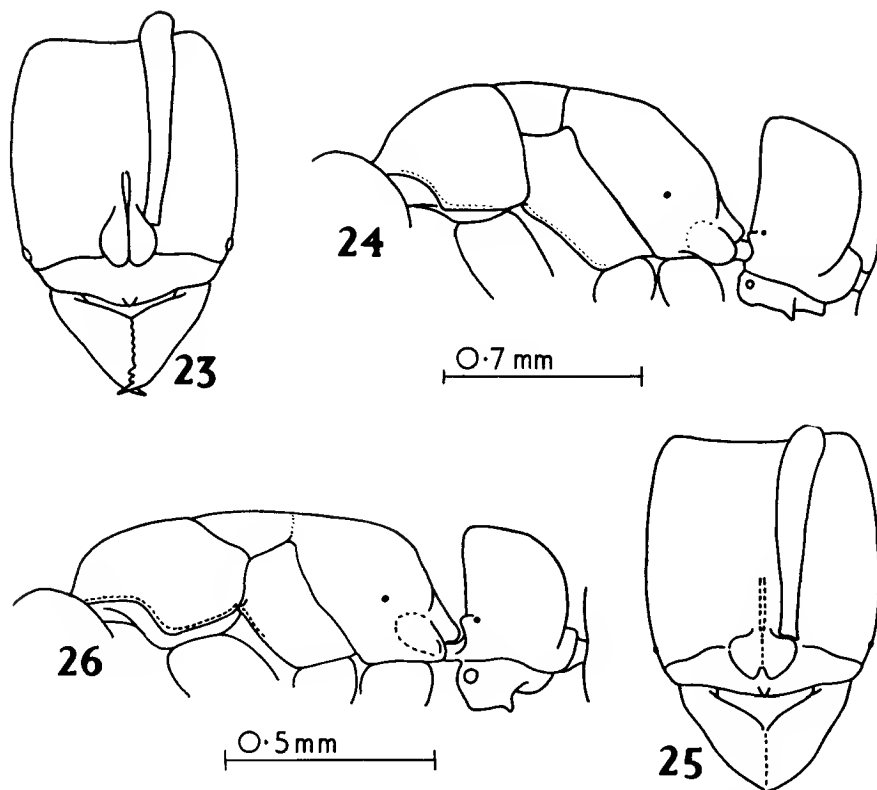
3. Petiolar node exceptionally broad—petiolar node index 92-98. This index does not exceed 90 in any other species.

Females of *P. alpha* are likewise characterized by large size, with very broad head and petiolar node.

Holotype worker. HL 0.94 mm; HW 0.83 mm; SL 0.77 mm; CI 88; SI 93; PW 0.66 mm; PNL 0.38 mm; PH 0.70 mm; DPW 0.64 mm; PNI 97. Mandibles with 3 well developed teeth occupying slightly less than apical 1/2 of masticatory border; basal 1/2 with 6 small, regular denticles. General form of head as in fig. 23; sides moderately convex, occipital border feebly concave. Median clypeal border with a small, acute, anteriorly directed tooth, about 0.02-0.03 mm long. Eyes small, strongly convex, maximum diameter *ca* 0.04 mm; each with about 6 or 7 minute, indistinct facets. Anterior point of eye situated about 0.90 \times distance from lateral occipital border to midpoint of anterior genal border. Scapes relatively very long, exceeding median occipital border by almost 1.5 \times their maximum thickness. No distinct antennal club differentiated, antennomeres increasing gradually in length and breadth towards apex; terminal segment slightly longer than 2 preceding together.

Mesosoma as in fig. 24. Inferior pronotal angles obtusely pointed. Mesometanotal and lateral mesonotal sutures distinctly incised. Posterolateral propodeal margins forming angles of about 70°, viewed from above. Sides of propodeum, from above, fairly strongly concave; declivity moderately so. Petiolar node very thick and wide; contained by 2 strongly arched faces: a vertical anterolateral one, and a transverse posterodorsal one. These 2 faces separated by a distinct angled edge. Viewed from above the node forms an almost perfect half-circle, the posterior border almost straight. Subpetiolar process relatively low, fenestra small, circular; posterolateral teeth small, moderately divergent.

Mandibles smooth and shining, with a few scattered punctures. Clypeus irregularly shagreened. Frons opaque, with a close cover of shallow, irregular foveolate punctures,



Figs. 23-26. *Ponera alpha* n. sp., worker (Holotype): 23, head; 24, mesosoma and node (scale line=0.7 mm). *Ponera selenophora* Emery, worker (Karema, S. E. New Guinea): 25, head; 26, mesosoma and node.

about 0.01 mm in diameter; so closely spaced that inter-punctural areas form a moderately fine raised reticulum. Scapes closely and coarsely punctate. Pronotum moderately shining, finely and shallowly transversely rugulose; the rugulae almost effaced, mixed with fine punctures. Mesonotum markedly more opaque than remaining mesosomal dorsum, coarsely and closely punctate, somewhat like frons, but with a longitudinal trend to inter-punctural reticulum. Mesepisternal surface resembling pronotum, but rugulae more clearly marked and irregularly broken, not mixed with punctae, sculptural trend longitudinal. Similar sculpturing extends back over metepisternal area, below and in front of propodeal spiracle. Dorsum of propodeum moderately shining, with scattered punctures, sides smooth and very shiny. Declivitous face of propodeum, and posterodorsal face of node strongly shining, with a very fine, superficial scale-like microsculpture, visible in reflected light. Trend of this sculpturing transverse on propodeum, longitudinal on node. Anteroventral face of node shining, with scattered fine puncturation. Gaster similarly sculptured; a narrow strip on posterior margin of 1st gastric tergite finely shagreened.

Moderately long erect yellowish hairs plentiful on mandibles, clypeus, frontal lobes, scapes, entire dorsal surface of mesosoma, apex and sub-petiolar process of node, and en-

tire gaster, where they are especially abundant. Pubescence almost everywhere abundant, fine and adpressed, longest in pilose areas, sparse on sides of mesosoma.

Entire body very dark brown, almost black; apices of frontal lobes, sub-petiolar process and tip of gaster infuscated. Fore-coxae dark brown, remainder of legs, mandibles and antennae dull reddish brown.

TYPE LOCALITY. NE NEW GUINEA: Kunai Creek, 1300 m, SW side of Bulolo River valley, near Wau. The holotype was collected from a leafmold berlesate taken in a disturbed fragment of midmountain rain forest in a dark damp roadside gorge, VI.1962 (RWT acc. 1966). Known only from the type locality (see fig. 36).

Paratype workers. 31 paratype workers collected with the holotype have the following dimensions: HL 0.85–0.94 mm; HW 0.76–0.85 mm; SL 0.70–0.77 mm; CI 86–93; SI 85–95; PW 0.57–0.68 mm; PNL 0.32–0.39 mm; PH 0.59–0.70 mm; DPW 0.54–0.65 mm; PNI 92–98. The relative proportions of the several dimensions vary in a manner similar to that of members of the *Ponera coarctata* group. Pronotum width and petiole height approximately isometric, relative to head width. Petiolar node width positively allometric ($k \approx 0.85$), while head length and scape length are both negatively allometric (k between 1.3 and 1.4). Size of eyes may range down to slightly less than 0.03 mm maximum diameter, and posterior mandibular denticles may number 6 to 8. Faceting of eyes very indistinct in this species, and a facet count is very difficult. Under low magnifications (less than 100 \times) the eyes may appear as large, rather irregularly molded single facets.

Palpal formula (3 paratypes dissected): *Maxillary 2: Labial 2.*

The mesosomas of many paratypes have partially collapsed in preservation, so that the concavity of the sides of the propodeum is exaggerated, and the pronotum, viewed from above, appears to have the inferior angles turned outwards.

Paratype ♀♀. 3 dealates collected with the holotype have the following dimensions and indices: HL 0.93–0.96 mm; HW 0.85–0.87 mm; SL 0.77–0.78 mm; CI 90–91; SI 90–91; PW 0.72–0.75 mm; PNL 0.35–0.36 mm; PH (1 measurement) 0.70 mm; DPW 0.67–0.70 mm; PNI 92–97. Maximum diameter of eye 0.17–0.18 mm; ocular index 20–21. Palpal formula (dissected): *Maxillary 2: Labial 2.* General form of mandibles, head, clypeus, and antennae as in worker. Anterior border of eyes situated about 0.40 \times their length from lateral genal border, ocelli well developed. Mesosomal structure complete. Mayrian furrows absent, parapsidal lines distinct. Scrobal suture feebly marked. Petiolar node slightly thinner in side view than in worker; forming slightly less than a half-circle in dorsal view.

Sculpture generally as in worker. Punctuation of head slightly finer, the overall effect more shagreened. Scutellum coarsely punctate; metanotum smooth and shining. Entire sides and dorsum of propodeum finely longitudinally rugulose. Rugulae somewhat effaced in center of area above propodeal spiracle, the surface here moderately shining. Scale-like microsculpture on posterior faces of propodeum and node, more distinct than in worker, especially on node.

Color, pilosity, and pubescence as in worker.

ADDITIONAL PARATYPE MATERIAL. A small colony fragment of *alpha* was collected under bark on a fairly sound rotting branch immediately adjacent to the spot where leafmold had been previously collected (RWT acc. 1925). This probably represented the remains of the holotype colony; it included 4 workers, 3 dealate ♀♀, about 10 larvae, of at least

4 instars, and a few eggs. The worker and ♀ measurements fall within the ranges of the paratype series discussed above.

Immature stages. The larva has 6 pairs of glutinous tubercles on the abdominal dorsum, as do all other known Indo-Australian *Ponera* species. The pupae are not known.

TYPE DEPOSITION. The holotype 1 ♀ paratype, and most paratype workers in MCZ collection (Type No. 30918). Additional paratypes in the following collections: AMNH, Bishop (including ♀), BMNH, CAS, CSIRO (including ♀), Emery Coll., Forel Coll., Paris Mus., USNM, and Yasumatsu Coll.

RELATIONSHIPS. *P. alpha* is almost certainly the most primitive known Indo-Australian *Ponera*, and many of its characters are considered here to be primitive for the genus. It is linked to the apparently more derived species through *P. selenophora*.

5. *Ponera selenophora* Emery Figs. 25, 26, 34.

Ponera selenophora Emery, 1900, Természetr. Füzet. Stet. **23**: 317, pl. 8, figs. 4-6, worker.

Type locality: Lemien, near Berlinhafen (Aitape), NE New Guinea.—Wilson, 1957,

Bull. Mus. Comp. Zool., Harv. **116** (6): 382, fig. 3, worker, redescription, distribution.

Selenopone selenophora: Wheeler, 1933, Am. Mus. Nov. **672**: 21.

DIAGNOSIS. A New Guinea and northern Australian species, apparently widespread in lowland forested areas. Not referable to any species group recognized here, but close to *P. alpha*. The following characters are diagnostic: size moderately large (head width 0.59-0.65 mm). Head broad (cephalic index 88-92), with a more or less distinct median clypeal tooth and small eyes (2-3 indistinct facets); scapes exceeding median occipital border by up to 0.5× their maximum thickness, antennal club not segmentally differentiated. Mesometanotal suture weakly incised, absent in some specimens. Propodeal and petiolar node structure much as in *alpha*, the node narrower (petiolar node index 85-89), and the subpetiolar process larger.

Additional description. My present concept of *P. selenophora* may be too extensive. A complex of 2 or 3 closely related species may be represented in the material studied here. The only known New Guinean specimens, apart from the types, are those used by Wilson; I have not seen them all, however, I have seen 2 workers (one an extreme callow) from Karema, Brown River, SE New Guinea, and single workers from the lower Busu River, NE New Guinea, and Skull Creek, N. Queensland, Australia. The Karema specimens were compared with Emery's syntypes of *selenophora* by Wilson in 1955.

These specimens all seem referable to a single species, although they vary in the development of the mesometanotal suture, and intensity of the sculpturation, particularly on the mesosomal dorsum. The 3 collection localities are widely separated, but it seems that a single, variable species is represented here. In any case it would be presumptuous to name these forms as distinct species at present; future collecting in lowland forests in New Guinea and Cape York should clarify their true relationships.

The following notes and qualifications are additional to those of Wilson (1957).

1. Dimensions for the New Guinea material are: HL 0.65-0.69 mm; HW 0.59-0.63 mm; SL 0.52 mm; CI 88-92; SI 82-89; PW 0.45-0.49 mm; PNL 0.23-0.24 mm; PH 0.45-0.46 mm; DPW 0.40-0.42 mm; PNI 85-89. The Skull Creek specimen is slightly larger, but does not differ significantly in the major indices: HL 0.70 mm; HW 0.65 mm; SL 0.53

mm; CI 92; SI 82; PW 0.49 mm; PNL 0.25 mm; PH 0.48 mm; DPW 0.42 mm; PNI 86.

2. Mandibular dentition variable. In all specimens 3 large teeth occupy apical 1/2 of masticatory border, and these are followed by a series of large denticles. In the Karema callow the configuration of the denticles is similar to the syntype described by Wilson: "basal half (of border) occupied by two smaller teeth, one located midway between the basalmost of the apical teeth and the basal angle. In addition there are several irregular denticles in the inter-dentary spaces of the basal half of the border." This general plan is present in the other Karema specimen, but the posterior tooth/denticle series is much less irregular—it consists of 5 large denticles. The Busu specimen agrees with this last Karema one, and the Skull Creek individual, which has very worn mandibles with only traces of the denticles remaining, seems also to comply.

3. The clypeus of the Karema specimens bears a small (0.02 mm high) but distinct conical median tooth, the Skull Creek example has a short longitudinal carina in the middle of the clypeus; and the Busu River specimen has a slightly stronger carina, which almost traverses the clypeus.

4. The scapes exceed the median occipital border by about 0.5× their maximum thickness in the Karema specimens. In the Busu and Skull Creek ones they barely exceed the border.

5. The mesometanotal suture is almost obliterated on the mesosomal dorsum of the Karema example, a very faint trace being visible in some lights. The suture is not incised in the Skull Creek specimen, but here there is a distinct sculptural discontinuity between the mesonotum and propodeum. The Busu River specimen has a similar sculptural break, and in addition the suture is weakly incised.

6. The sculpturation is variable. That of the mandibles, head and antennae in the New Guinea specimens is as described by Wilson, the frons of the Skull Creek specimen is similarly densely and coarsely punctate, but the punctures are larger—up to approximately 1.5× the size of those in the New Guinea examples.

The mesosomal sculpturation in the Karema specimens is relatively light, as described by Wilson. The Busu River specimen has the disc of the pronotum moderately coarsely punctate, the individual punctures about 0.006 mm in diameter, separated by distances averaging a little more than half their maximum diameter; the sides of the pronotum are less heavily punctate than its dorsum, and there is a distinct faint transverse rugosity of the interpunctural surfaces. Mesonotal puncturation similar to that of pronotal disc, but with a distinct, though somewhat effaced, accompanying longitudinal rugosity. There is a distinct sculptural break along the mesometanotal suture, propodeal dorsum being rather finely and sparsely punctate. The sculpturing of the sides of the mesosoma is similar to that of the Karema specimens.

The mesosoma of the Skull Creek specimen is somewhat more heavily punctate than either of the New Guinea ones: pronotum subopaque, with a contiguous cover of shallow punctures about 0.01 mm in diameter. Mesonotum much as in Busu River specimen, slightly more coarsely and densely sculptured; propodeal dorsum slightly more coarsely and closely punctate. The mesonotal-propodeal discontinuity marked.

In all other features the samples show little variation and agree with the diagnosis for this species given above.

♂, ♀ and immature stages unknown.

DISTRIBUTION AND MATERIAL EXAMINED. NW NEW GUINEA: Maffin Bay (Wilson 1957). NE NEW GUINEA: Lemien, near Aitape (type locality) (Emery 1900); Lower Busu River, near Lae, 28.IV.1955 [E. O. Wilson, acc. 884 (wrongly cited as 564 in Wilson's paper)] MCZ. SE NEW GUINEA: Karema, near Brown River, 8-11.III.1955 (E. O. Wilson acc. 564). AUSTRALIA: *Queensland*: Skull Creek, Berlese funnel sample, leafmold, edge of swamp, 15.V.1953 (E. N. Marks) CSIRO.

ECOLOGY. It is probably significant that all records of *selenophora* are from low elevations. Wilson took it at the Brown River and Karema sites in primary rain forest. I did not encounter *selenophora* during almost 5 weeks collecting in New Guinea, but all but a few days were spent at much greater elevations. Considering known facts regarding the zoogeography of Pacific ants, *selenophora* will probably be more widespread in E. Melanesia.

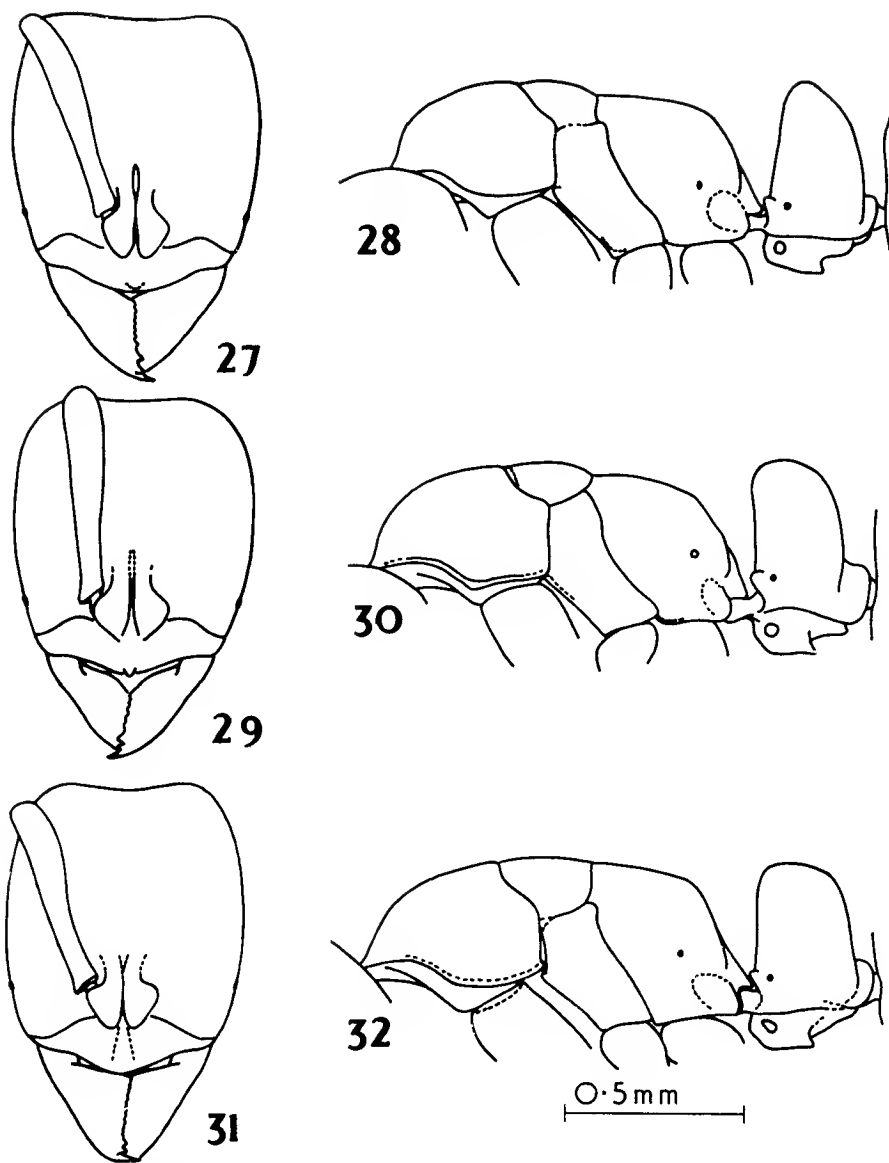
RELATIONSHIPS. *P. selenophora* is essentially a smaller version of *P. alpha*, with proportionately shorter scapes, and a narrower petiolar node (the similarities are evident in figs. 23-26). In *selenophora* the petiolar node is of almost exactly the same general (primitive?) plan as that of *alpha*, with distinct anterolateral and posterodorsal faces, separated by a curving angulate border. The Karema and Skull Creek specimens are similar to *alpha* in sculpturation, especially in the peculiar sculptural break between the mesonotum and propodeum. *Selenophora* may provide a link between *alpha* and the *sinensis* and *taipin-gensis* groups. The beginnings of several major tendencies, which seem to have been of general significance in the evolution of *Ponera* are evidenced when *selenophora* is compared with *alpha*. These include reduction in size, narrowing of the head and petiolar node, decrease in the number of eye facets, shortening of the scapes, loss of the mesometanotal suture and reduction in the sculptural intensity.

6. *Ponera xenagos* Wilson Figs. 27, 28, 36.

Ponera xenagos Wilson, 1957, Bull. Mus. Comp. Zool. Harv. **116** (6): 385, worker. Type locality: Tumnang, NE New Guinea (Holotype and paratypes examined—MCZ).

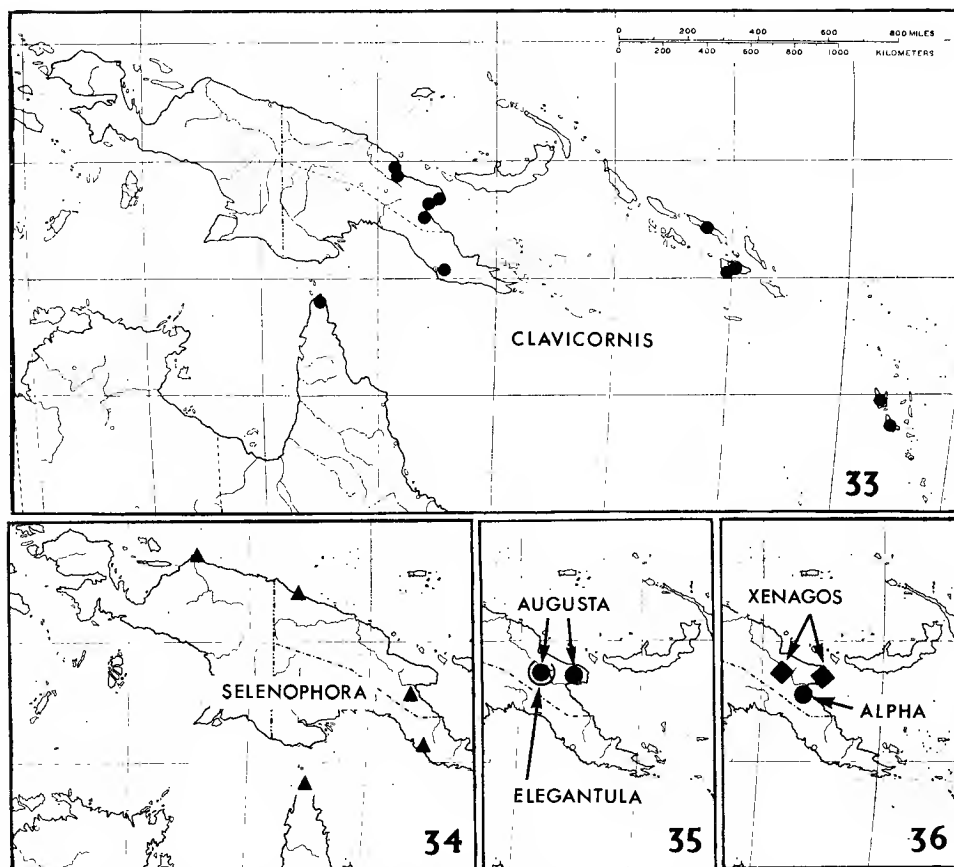
DIAGNOSIS. A New Guinean species, the largest known *Ponera* apart from *P. alpha*. Recognized by the combination of large size (head width 0.65-0.73 mm) with relatively broad head (cephalic index 84-90), vestigial medium clypeal tooth and relatively long scapes, which surpass the median occipital border by about 1/2 their maximum thickness. The eyes are small (4-5 indistinct facets), and no antennal club is differentiated. Posterolateral propodeal angles not markedly raised, and node with more rounded contours than in *alpha* or *selenophora*, although it still maintains the same basic form with arched anterolateral and posterodorsal faces.

Additional description and variation. I have specimens from two areas in eastern New Guinea—the holotype and 6 paratypes from localities on the Huon Peninsula, and 7 workers from Aiyura, Eastern Highlands District. These two series differ in the relative length of the antennal scapes, and thickness of the petiolar node; they are otherwise similar in structure. Considering their allopatric status and the known facts regarding variation in other *Ponera* species they are accepted as conspecific. Mean size differs between the two samples and it is possible that the morphological variation is due to differences in the al-



Figs. 27-32. Some larger *Ponera* species. *Ponera xenagos* Wilson, worker (Holotype): 27, head; 28, mesosoma and node. *Ponera chapmani* n. sp., worker (Holotype): 29, head; 30, mesosoma and node: *Ponera scabra* Wheeler, worker (Syntype): 31, head; 32, mesosoma and node.

lometric expression of the characters involved. The apparent geographical variation could thus be an artifact, for the smaller Huon workers may be from younger colonies than the Aiyura ones—colonies producing sub-maximum sized individuals. The true status of these forms can be determined only in the light of further information on intranidal and intra-



Figs. 33-36. Distribution of some Melanesian *Ponera* species. 33, *P. clavicornis* Emery; 34, *P. selenophora* Emery; 35, *P. elegantula* Wilson, *P. augusta* n. sp.; 36, *P. alpha* n. sp., *P. xenagos* Wilson.

deme allometric variation, and knowledge of geographically intermediate populations.

Similar variation in size and other, probably allometric, characters is noted below for *P. elegantula*, which is also known only from Huon Peninsula and Aiyura.

The Huon Peninsula Series. The general features were adequately summarized by Wilson (1957). The following characters include diagnostic details and those significant in analyzing the variation discussed above.

Wilson's dimensions for the complete type series of 12 workers were: HL 0.75-0.80 mm; HW 0.65-0.68 mm; SL 0.57-0.60 mm; CI 86-90; SI 83-89; PW 0.52-0.54 mm; DPW 0.40-0.44 mm. My shorter series of 7 types have the following additional dimensions: PNL 0.27-0.29 mm; PH 0.52-0.54 mm; PNI 80-84. General form as in figs. 27-28. Palpal formula: *Maxillary* 2: *Labial* 2 (inspected). Median clypeal denticle vestigial, a low obtuse tumosity. Scapes exceeding occipital border by about 1/2 their maximum thickness. Eyes small, with 3 to 5 indistinct facets. Mesometanotal and lateral mesonotal sutures distinctly incised.

Aiyura series. Dimensions (N=7): HL 0.77-0.83 mm; HW 0.65-0.73 mm; SL 0.60-0.65 mm; CI 84-89; SI 88-95; PW 0.52-0.57 mm; PNL 0.27-0.30 mm; PH 0.53-0.59 mm; DPW 0.41-0.46 mm; PNI 79-81. These specimens differ from the Huon Peninsula sample in their larger size, longer scapes, and narrower petiolar nodes. The relevant dimensions and indices are summarized in the following table:

Population	Mean HL	Mean CI	Mean SI	Mean PNI
Huon*	0.77 mm	87	87	82
Aiyura	0.80 mm	87	90	80

Note that the mean scape index and petiolar node index values are different in the two samples, but no difference in cephalic index is shown.

As shown above workers of *P. pennsylvanica* and *P. alpha* show positive allometry of scape length, and negative allometry of petiolar node width, relative to head width. Similar allometric relationships may be present in *xenagos*. Demonstration of such polymorphism in a single nest or population sample would support my procedure in considering these two forms as a single species.

Immature stages. Larvae from Aiyura have 3 pairs of dorsal abdominal glutinous tubercles, as usual in Indo-Australian *Ponera*; the worker pupae are enclosed in cocoons (other castes not available).

MATERIAL EXAMINED. NE NEW GUINEA: *Huon Peninsula*: Tumnang, 1500 m (type locality), 14-15.IV.1955 (E. O. Wilson), 8 type workers. *Eastern Highlands*: Aiyura, 2000 m, 11.VII.1962, 7 workers (R. W. Taylor acs. 2162, 2164-5) MCZ, CSIRO.

ECOLOGY. Wilson's specimens were taken in partial clearings beside trails in dense mid-mountain rain forest. He found one nest at each site, under loose bark on a rotting stump at Tumnang, and on the upper surface of a large rotting log at Ebaabang. My Aiyura samples were taken in disturbed midmountain forest, nesting in rotting logs at the "passalid" or "zoraptera" stages of decay.

RELATIONSHIPS. *P. xenagos* is probably akin to the two preceding species, but various features mark it as a more derived form. These include the reduced sculpturation and the less marked angulation of the propodeum and node. This species is at approximately the same grade as the succeeding group of *P. scabra*.

Ponera scabra Group

The following two species, *chapmani* and *scabra*, are apparently related. Structurally they are at about the same grade as *P. xenagos*, and could perhaps be affiliated with it at the species group level. They are fairly large (head width 0.61-0.67 mm), with a tendency towards reduction of the median clypeal tooth in smaller specimens. The scapes are long, the funiculus lacks a differentiated club; and the eyes are small. The propodeal angles are not as strongly marked as in *alpha* or *selenophora*, and the contours of the node are more rounded, much as in *xenagos*. The angle between the dorsal and posterior faces of the node of *scabra* is fairly marked so that the two faces are more discreet than in most primitive *Ponera*, where a continuous arched postero-dorsal face is seen. The head is narrower than that of *xenagos* (cephalic index 78-85) and the sculpturation more dis-

* Based on holotype and 6 paratypes available here.

tinctly developed. Females of *chapmani* have peculiar wing venation, unlike that of all other known *Ponera*, except the distantly related *P. swezeyi* (see below). The wing venation of *scabra* is unknown. Males, larvae and pupae are not known for either of these species.

7. *Ponera chapmani* Taylor, new species Figs. 6, 29-30.

DIAGNOSIS. Known only from the Philippine island of Mindanao. Easily recognized by the combination of large size (head width 0.65-0.67 mm in worker, 0.67-0.68 mm in ♀), compact propodeal form without strongly angled posterolateral edges, presence of transverse striae on lower parts of declivitous face of propodeum and posterior face of node, presence of a distinct median clypeal denticle, and long scapes which slightly exceed the median occipital border (scape index 91-92).

Apparently close to the Japanese *P. scabra*, but distinguished by the characters given in the key above, and in the comparative diagnosis under *scabra* below. *Chapmani* is much larger than the other known Philippine *Ponera* species (*P. oreas*).

Holotype worker. HL 0.79 mm; HW 0.67 mm; SL 0.61 mm; CI 85; SI; PW 0.53 mm; PNL 0.28 mm; PH 0.57 mm; DPW 0.43 mm; PNI 81. Mandibles with 3 well developed teeth occupying approximately apical 1/2 of masticatory border. Remainder of border with 5 or 6 distinct large denticles. Head as in fig. 29, moderately broad with almost straight sides and slightly concave occipital border. Clypeus with a distinct blunt median tooth about 0.03 mm high. Eyes small, not markedly convex, their maximum diameter about 0.04 mm, with 4 or 5 indistinct facets; situated approximately 0.85× the distance from lateral occipital border to mid-point of anterior genal border. Scapes long, exceeding median occipital border by a distance equal to about 0.25× their maximum thickness, when laid back along head. No distinct antennal club differentiated, antennomeres increasing regularly in length and breadth towards apex; apical segment almost as long as the 3 preceding together.

General form of mesosoma as in fig. 30, lateral mesonotal and dorsal mesometanotal sutures distinctly incised. Posterolateral angles of propodeum not markedly pronounced, forming blunt angles of about 90° when viewed from above. Lateral faces of propodeum, viewed from above, almost straight, converging slightly anteriorly; declivitous face straight to feebly concave. Petiolar node as in fig. 30. Subpetiolar fenestra moderately large, circular; posterolateral teeth strong, moderately acute. Dorsal face of node, viewed from above, almost oval. Posterolateral angles of node broadly rounded, its posterior face straight to feebly convex.

Mandibles smooth and shining. Clypeus moderately shining, irregularly punctate. Front of head opaque with a close cover of coarse, more or less foveolate punctures, about 0.01 mm in diameter. Scapes fairly coarsely and closely punctate. Occipital area of head and entire pronotum moderately shining, with scattered fine punctures. Mesonotum semi-opaque with coarse foveolate punctures about 0.01 mm in diameter, separated by distance equal to approximately 1/2 their maximum diameter. Dorsum of propodeum moderately shining, with punctures similar to those of mesonotum, but more widely spaced at distances about equal to their maximum diameter. Sides of mesosoma moderately shining, with scattered punctae. Lower 1/2 of mesepisternum and entire metepisternal area fine-

ly longitudinally striate-rugose; a few broken fragments of such sculptures on side of propodeum, above spiracle. Declivitous face of propodeum shining with a cover of moderately spaced transverse striae, which are partly obliterated in the middle of upper 1/2 of face, which is smooth and shining. A few remnants of similar longitudinal striae above effaced area. Node moderately shining, scattered fine irregular punctae on dorsal and anterolateral faces, posterior face generally shining on upper 1/2, but transversely arched-striate-rugose on lower portion. Arched striae of posterior face of node continued at sides onto lower posterior parts of its lateral faces, and from there down over posterior 1/2 of subpetiolar process; trend of sculpture in these areas almost vertical. First gastric tergite subopaque, fairly coarsely and closely punctate, with a scaly appearance, due to individual punctures being deep anteriorly and barely depressed below the interpunctural surface posteriorly. Second gastric tergite similarly but more finely sculptured.

Pilosity moderately abundant, a few erect hairs on mandibles, clypeus, frontal lobes, scapes, dorsum of mesosoma, declivitous face of propodeum. More abundant sub-erect hairs on dorsum of node, and entire gaster. Pubescence everywhere moderately abundant, least so on sides of mesosoma, node and gaster. Color dull medium reddish brown; frons, dorsal faces of propodeum and 1st 2 gastric segments more darkly infuscated. Legs, mandibles, antennae and tip of gaster rich orange-brown.

Paratype workers. 3 paratype workers from the same series as holotype with following dimensions and indices: HL 0.77-0.78 mm; HW 0.65 mm; SL 0.60 mm; CI 83-84; SI 92; PW 0.52-0.53 mm; PNL 0.26-0.27 mm; PH 0.55-0.56 mm; DPW 0.41-0.42 mm; PNI 79-80. These specimens closely resemble the holotype. The eyes may range up to a maximum diameter of 0.05 mm, with 4-6 facets; posterior mandibular denticles range down to 4 in number; and scapes may exceed median occipital border by up to 0.5× their maximum thickness. Palpal formula (1 specimen dissected); *Maxillary* 2: *Labial* 2.

Paratype ♀♀. A single dealate and 8 alates from the same series as holotype (presumably collected from the same colony) with following dimensions and indices: HL 0.79-0.81 mm; HW 0.67-0.68 mm; SL 0.62-0.63 mm; CI 83-86; SI 91-94; PW 0.63-0.64 mm; PNL 0.28-0.30 mm; PH 0.61-0.63 mm; DPW 0.47-0.48 mm; PNI 74-76. Maximum diameter of eye 0.21-0.23 mm, ocular index 29-30. Palpal formula (1 specimen dissected): *Maxillary* 2: *Labial* 2. Differing from the worker in the usual characters of full sexuality. Structure of head, clypeus, mandibles and antennae as in worker; scapes exceeding occipital border by about 0.5× their maximum thickness. Anterior extremity of compound eyes situated 1/3-1/2 their maximum diameter from midpoint of anterior genal border. Mesosomal structure complete, inferior pronotal angles bluntly pointed; parapsidal furrows distinct, notaulices absent. Forewing venation (fig. 6) unique among known larger *Ponera* in that the 2nd abscissa of Rs+M arises distal to anterior base of medio-cubital cross-vein (m-cu). Propodeal angles as in worker, node thinner, more or less transversely elongate oval in dorsal view. Sculpture, color, pilosity and pubescence in general as in worker; mesosomal sculpture a little more intense, especially longitudinal rugosity of metepisternal areas and sides of propodeum. Transverse striate-rugosity of declivitous propodeal face more distinct than in worker and not effaced in center. Sculpture of metasoma as in worker.

TYPE LOCALITY. The type series was located in the J. W. Chapman collection (MCZ): PHILIPPINE IS.: Mindanao: Mt. Apo, 1500-1800 m (C. F. Clagg), no ecological details

cited, probably collected in rain forest. This species is named for the late Dr James W. Chapman, in recognition of his contributions to Philippine myrmecology and entomology.

TYPE DEPOSITION. Holotype and paratypes (worker and ♀) in MCZ (Type No. 30919); paratypes in BISHOP and CSIRO (workers and ♀♀), BMNH and USNM (♀♀ only).

RELATIONSHIPS. *Ponera chapmani* may form a super-species with the apparently closely related Japanese *P. scabra*. There is also a general resemblance to the New Guinean *P. xenagos*. These species appear related to the eastern nearctic and European palearctic members of the *coarctata* group, which have peculiar larval and male characters. Unfortunately the relevant characters cannot be checked, due to lack of these stages. It would be of interest to know whether the peculiar wing venational features of *chapmani* are present in *scabra*.

8. *Ponera scabra* Wheeler Figs. 31, 32.

Ponera scabra Wheeler, 1928, Boll. Lab. Zool. Portici **21**: 99-100, worker, ♀. Type locality: Mt Maya, Honshu, Japan (syntypes examined—MCZ, AMNH).—Santschi, 1937, Bull. Soc. Ent. Belg. **77**: 364, gynecoid worker, distribution; 1941, Mitt. schw. ent. Ges. **18**(4/5): 273.—Wilson, 1957, Bull. Mus. Comp. Zool. **116** (6): 381, further description of syntype workers.

Ponera (*Hypoponera*) *scabra*: Santschi, 1838, Ann. Soc. Ent. France **43**: 79.

The records of *P. scabra* published in the important ecological studies of Hokkaido ants by Hayashida (1957, 1960) were in fact based on incorrectly determined specimens of *P. japonica*, which were generously made available for this study by Dr Hayashida. For further information see below under *P. japonica*.

DIAGNOSIS. A Japanese species closely related to, and possibly cognate with, *P. chapmani*. Distinguished in general from other *Ponera* species by the combination of moderately large size (head width 0.61-0.64 mm in worker, 0.71-0.74 mm in ♀), heavy sculpturing, and long scapes, which almost exactly reach the median occipital border. Readily differentiated from the only other known Japanese species, *P. japonica*, by its larger size (head width 0.42-0.50 in *japonica*) and heavier sculpturation. *P. scabra* may be differentiated from the related *chapmani* by the following characters:

Worker:

1. The 3 large apical mandibular teeth occupy about 1/3 of the masticatory border, and are followed by a series of 10-12 minute denticles.

2. Median clypeal denticle much less pronounced, at least in smaller specimens (see below).

3. Scapes relatively short; when laid back along head they almost exactly reach the median occipital border.

4. Head narrower (cephalic index 78-83 opposed to 83-85 in *chapmani*).

5. Mesometanotal suture much less distinctly incised, although indicated by a break in sculpturation.

6. Posterior border of node, viewed from above, distinctly concave. Node relatively wide (petiolar node index 84-89 opposed to 79-80 in *chapmani*).

7. Sculpturation of mesosoma and node much more pronounced; striae of propodeal

declivity and posterior face of node lacking (see Wilson's description).

The posterior face of node with fine transverse superficial "scaly" sculpturation, like that on propodeal declivity of *P. alpha*, but more distinctly developed. This sculpturation, which probably represents a vestigial striate-rugosity, is more distinct on the lower 1/2 of face than above.

♀. Differentiated from ♀ of *chapmani* by larger size and the same mandibular, scape, nodal and sculptural characters which distinguish the worker. Compound eye distinctly smaller, its maximum diameter 0.25 to 0.26 × head width, opposed to 0.29 to 0.30 × HW in *chapmani*. Wing venation unknown (unfortunately; considering the peculiar venation of *chapmani*).

Additional description. The following notes are based on 7 syntype workers and 2 dealated syntype ♀♀ from the MCZ and AMNH collections. An additional unstudied syntype worker is in the USNM collection (M. R. Smith, *in litt*). Wheeler presumably returned some of his types to Silvestri and it is not known whether he designated a holotype. Accordingly, no lectotype selection has been made here.

Syntype workers (figs. 31, 32). In addition to the features indicated in the diagnosis above the following details should be noted: HL 0.77-0.80 mm; HW 0.61-0.64 mm; SL 0.56-0.59 mm; CI 78-80; SI 90-93; PW 0.46-0.50 mm; PNL 0.26-0.28 mm; PH 0.49-0.53 mm; DPW 0.39-0.43 mm; PNI 84-88.

Eyes about 0.03 mm in diameter, with 3-5 indistinct facets. Median clypeal tooth at best vestigial, represented by a low flat tumosity; a little more distinct in larger specimens. Antennal club as described for *chapmani*. General form of propodeum as in *chapmani*; petiolar node somewhat bulkier (cf. figs. 30, 32).

Additional workers. 2 workers from Hikosan, Kyushu (K. Yasumatsu) have the following dimensions: HL 0.78 mm, 0.84 mm; HW 0.64 mm, 0.70 mm; SL 0.57 mm, 0.61 mm; CI 82, 83; SI 89, 87; PW 0.49 mm, 0.55 mm; PNL 0.25 mm, 0.30 mm; PH 0.51 mm, 0.55 mm; DPW 0.44 mm, 0.47 mm; PNI 89, 85. These specimens agree well with the syntypes but have relatively high CI and low SI values. The larger specimen is probably slightly gynecoid; its eyes are about 0.05 mm long with 7 rather distinct facets, and the median clypeal denticle is well developed, as in ♀. The palpal formula (smaller specimen dissected): *Maxillary* 2: *Labial* 2.

Syntype ♀♀. (N=2): HL 0.87 mm; HW 0.71 mm, 0.74 mm; SL 0.64 mm, 0.65 mm; CI 82, 85; SI 90, 88; PW 0.60 mm, 0.66 mm; single measurements (1st specimen) for PNL 0.30 mm and PH 0.60 mm; DPW 0.51 mm, 0.55 mm; PNI 85, 83; maximum diameter of compound eye 0.18 mm; 0.19 mm; ocular index 25, 26.

Differing from the workers in the usual characters, and from other *Ponera* ♀♀ by the characters of the diagnosis above. The palpal formula has not been checked.

♂. Larval and pupal material has not been available for study.

DISTRIBUTION AND MATERIAL EXAMINED. All known records of *P. scabra* are given here. I have seen none of the Santschi material so cannot vouch for his records. JAPAN: *Honshu*: Kamakura (Wheeler 1928); Mt Maya (*type locality*), 28.VI.1925 (Silvestri) MCZ, AMNH; Minoo (=Mino), Osaka (Santschi 1941). *Kyushu*: Hikosan (Buzen), IX.1939, XIII. 1940 (K. Yasumatsu) MCZ; Moji-kiu, Shiroyama (Santschi 1937).

RELATIONSHIPS. See above under *P. chapmani*.

Ponera sinensis Group

The following two species, *oreas* (Philippines) and *sinensis* (Hong Kong), are closely related and probably cognate. They are considerably smaller than any of the preceding species (head width 0.47–0.54 mm) and the head is much broader than in other *Ponera* of similar size (cephalic index 89–95). A median clypeal denticle is lacking and the eyes are small with 3–6 facets. The scapes reach or slightly exceed the median occipital border and the club is at most feebly marked, although there is a distinct tendency for it to be segmentally differentiated—in most specimens it is fairly distinctly 4 or 5 segmented. The mesometanotal suture is sharply incised, and the form of the propodeum and petiole generally as in *P. xenagos*. These species are probably descended from a stock much like *P. xenagos*, from which they differ mainly in their smaller size, high cephalic indices, and in the tendency for differentiation of the antennal club. The latter character is of frequent occurrence among the smaller species of *Ponera*, and has apparently been separately evolved in several groups.

9. *Ponera oreas* (Wheeler) Figs. 40–42.

Selenopone oreas Wheeler, 1933, Amer. Mus. Novitates **672**: 20–21, fig. 8, worker. Type locality: Guernos Mts, 1300 m, near Dumaguete, Negros Oriental, Philippine Is. (Syntypes examined—MCZ coll.).

Ponera oreas: Wilson, 1957, Bull. Mus. Comp. Zool. **116**(6): 381, redescription of syntypes.

DIAGNOSIS. Known only from the island of Negros Oriental, Philippine Is. Closely related to *P. sinensis* and distinguished from it by characters given below under *sinensis*.

Additional description. The following notes are based on the syntype series—4 workers and a ♂, plus an additional 29 workers and 2 dealate ♀♀ from the J. W. Chapman collection (MCZ). All material is from the vicinity of Dumaguete, Negros.

Worker. (figs. 40–42).

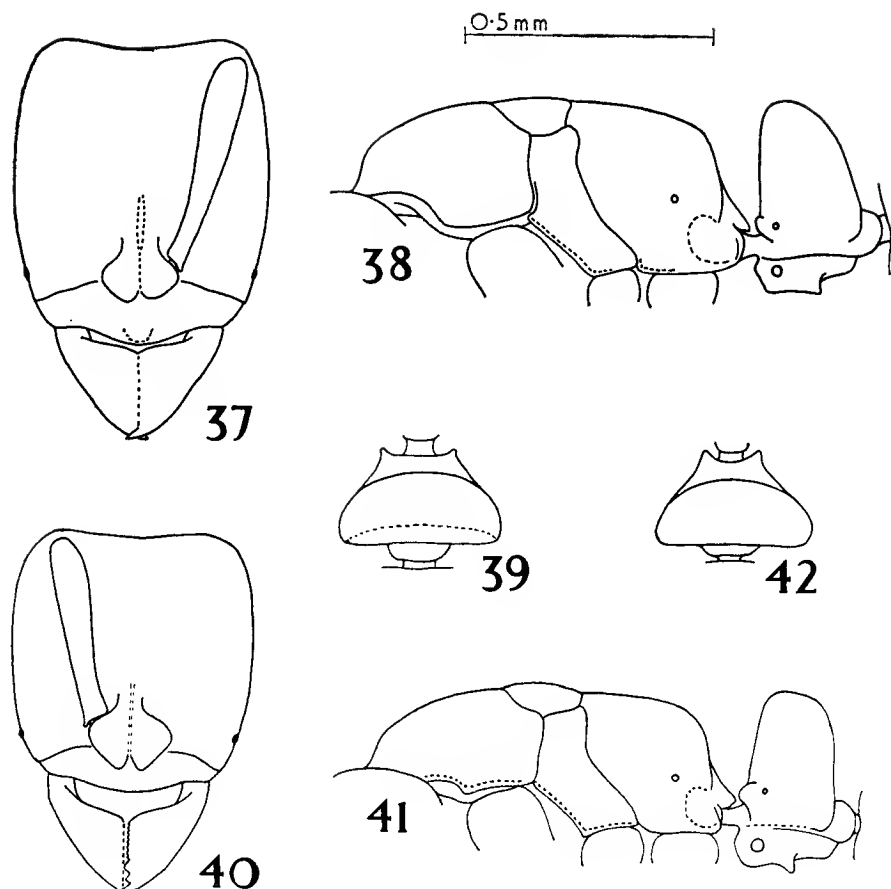
1. HL 0.50–0.54 mm; HW 0.47–0.51 mm; SL 0.38–0.41 mm; CI 92–95; SI 78–81; PW 0.35–0.39 mm; PNL 0.15–0.19 mm; PH 0.35–0.37 mm; DPW 0.29–0.33 mm; PNI 82–85.

2. Mandibles with 3 large teeth occupying apical 1/2 of masticatory border, followed by an irregular series of 7 or 8 minute indistinct denticles. Palpal formula: *Maxillary* 2: *Labial* 2 (2 specimens dissected). Clypeus completely lacking a median tooth. Eyes small, with 3 to 6 indistinct facets, situated about 0.89× the distance from the lateral occipital border to the midpoint of the anterior genal border. Scapes reaching, or very slightly exceeding, median occipital border. Antennal club rather indistinctly 4-segmented, apparently undifferentiated in some specimens. (It was described as 5-segmented by Wheeler, but see Wilson's (1957) notes.) Terminal antennomere slightly longer than the 2 preceding together.

3. Mesometanotal and lateral mesonotal sutures clearly defined. Posterolateral edges of propodeum slightly raised, forming angles of about 80° in dorsal view.

Other characters as in the comparative discussion below under *P. sinensis*.

♀. Two worker-associated dealates have the following dimensions: HL 0.54 mm, 0.57



Figs. 37-42. Group *Ponera sinensis*. *Ponera sinensis* Wheeler, worker (Holotype): 37, head; 38, mesosoma and node; 39, node dorsal view. *Ponera oreas* (Wheeler), worker (Holotype): 40, head; 41, mesosoma and node; 42, node, dorsal view.

mm; HW 0.52 mm, 0.54 mm; SL 0.41 mm, 0.43 mm; CI 96, 94; SI 89; PW 0.43 mm, 0.46 mm; PNL 0.20 mm, 0.21 mm; PH 0.40 mm, 0.42 mm; DPW 0.36 mm, 0.38 mm; PNI 84, 83; maximum diameter of eye 0.13 mm, 0.14 mm; ocular index 25, 26; palpal formula not determined. Differing from the worker in the usual features. Scapes extending posteriorly as in worker, parapsidal lines distinctly impressed, mesosomal structure complete, node not very markedly narrowed above relative to that of worker. The diagnostic characters of the *sinensis* complex workers are probably generally applicable to the ♀♀; namely medium size, broad head, and feebly differentiated antennal club.

♂. A single specimen originally mounted with the syntype workers has the following dimensions: HL 0.46 mm; HW across eyes 0.50 mm; CI 109; WL 0.89 mm; PNL 0.19 mm; PH 0.25 mm; DPW 0.19 mm; maximum diameter of eye 0.23 mm; ocular index 46; palpal formula (dissected): *Maxillary* 3: *Labial* 2. General structure of head, mesosoma, antennae, legs and node, as in *P. pennsylvanica*. Terminal abdominal sclerites and genitalia conform-

ing to general plan for the genus. Pygidial spine somewhat longer than in *pennsylvanica*; basal ring of genital capsule with plane of genital foramen almost oblique to its longitudinal axis, so that the ring is nearly as long ventrally as it is dorsally. Dorsal process of paramere almost as long as ventral one, digitate in side view, with its lower edge thickened. This process in dorsal view is thin and arcuate, inclined mesally. Volsellae and penis valves as in *pennsylvanica*, the posterodorsal angle of the latter almost right angled. Wing venation of "coarctata type." Color medium dark brown.

DISTRIBUTION AND MATERIAL EXAMINED. PHILIPPINE IS.: *Negros*: Guernos Mts, near Dumaguete, 1200 m, (F. X. Williams) syntype workers and ♂ (MCZ). Vicinity of Dumaguete, a number of workers collected by J. W. Chapman, with labels bearing the word 'camp', along with one of the following dates: 31.III., 18.V.1927; 2, 3, 19, 20.IV.1931.

The types and most of the other specimens are deposited in the MCZ collection, and duplicates of the additional material are in BISHOP, BMNH, CSIRO (including ♀) and USNM.

RELATIONSHIPS. See above under species group diagnosis.

10. *Ponera sinensis* Wheeler Figs. 37-39.

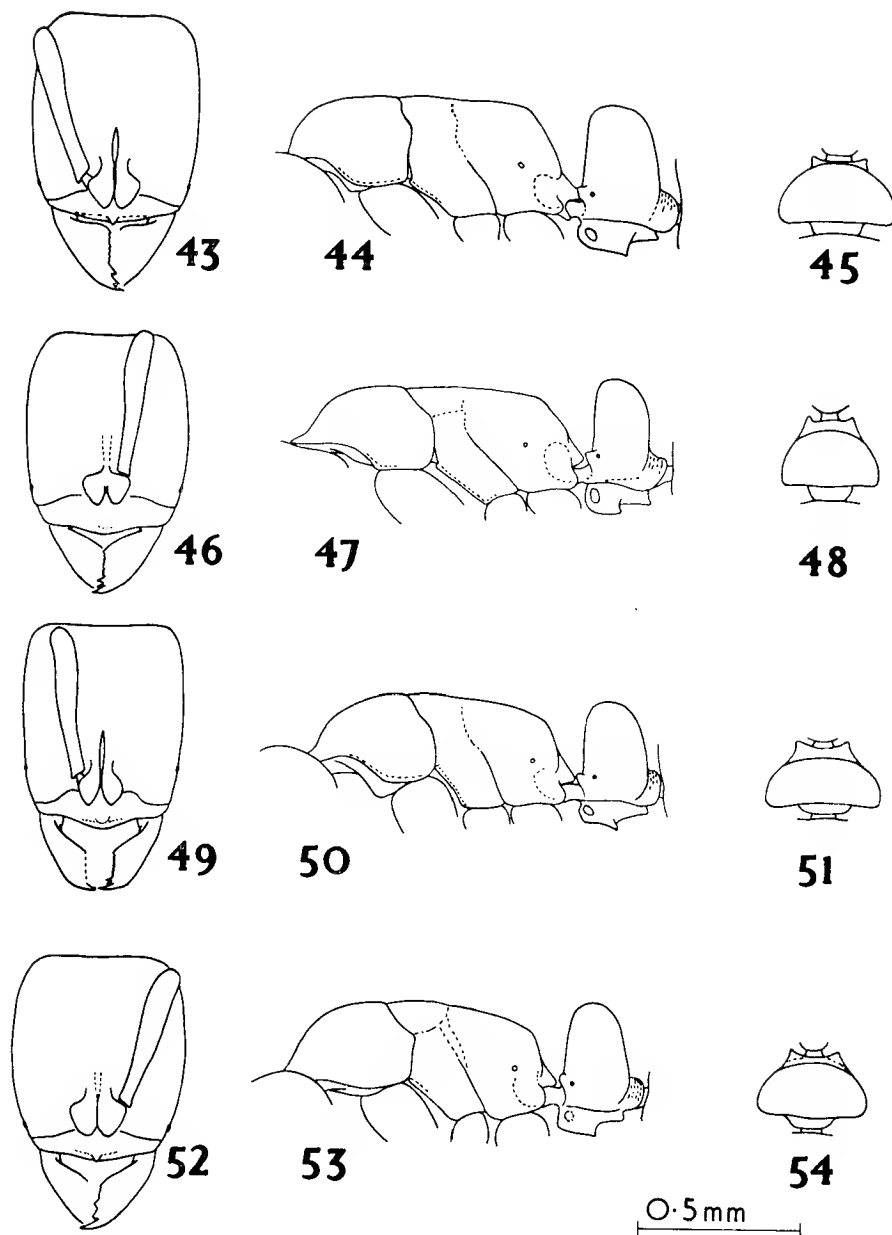
Ponera sinensis Wheeler, 1928, Boll. Lab. Zool. Portici **22**: 6-7, worker. Type locality: Hong Kong (Holotype examined—MCZ coll.).—Wilson, 1957, Bull. Mus. Comp. Zool. **116** (6): 384, redescription of holotype.

DIAGNOSIS. Known only from unique holotype. The nominate species of the *P. sinensis* group, which also includes the similar and closely related *P. oreas*. *P. sinensis* may be distinguished from *oreas* by the following characters:

1. Larger size (head width 0.54 mm, opposed to 0.47-0.51 mm in *oreas*)
2. Narrower head (cephalic index 89 against 92-95).
3. Slightly higher scape index (83; 78-81 in *oreas*)
4. Antennal club indistinctly 5-segmented, where it is 4-segmented in *oreas*.
5. The 3 apical mandibular teeth occupy only the anterior 2/5 of masticatory border; no posterior denticles delimited (this is possibly an artifact due to wear since the apical teeth look well worn on the holotype!).

6. Cephalic sculpturation consisting of a close cover of punctures about 0.006 mm in diameter, separated by distances of about 1/2 their average diameter. In *oreas* the head is distinctly more dull, with sculpturation best described as 'shagreening.' It consists of similarly sized punctures, but they are almost contiguous, with very little exposed interpunctural surface. Remaining sculpturation similar in 2 species, except that most *oreas* workers have a shining, almost apunctate, median posterior strip on the propodeal dorsum; this area is evenly punctate in *sinensis*.

My measurements of the holotype differ slightly from Wilson's: HL 0.61 mm; HW 0.54 mm; SL 0.45 mm; CI 89; SI 83; PW 0.41 mm; PNL 0.20 mm; PH 0.39 mm; DPW 0.35 mm; PNI 85. Note that certain characters cited above contradict those of Wheeler's description, which is inaccurate in places. The eyes of the holotype are *not* one-faceted as he claimed, but the visible left one, at least, has 4 fairly distinct facets. The oral palpi have not been dissected.



Figs. 43-54. Group of *Ponera taipingensis*. *Ponera taipingensis* Forel, worker (Lectotype): 43, head; 44, mesosoma and node; 45, node dorsal view. *Ponera syscena* Wilson, worker (Holotype): 46, head; 47, mesosoma and node; 48, node, dorsal view. *Ponera colcensis* Mann, worker (Holotype): 49, head; 50, mesosoma and node; 51, node, dorsal view. *Ponera loi* n. sp., worker (Holotype): 52, head; 53, mesosoma and node; 54, node, dorsal view.

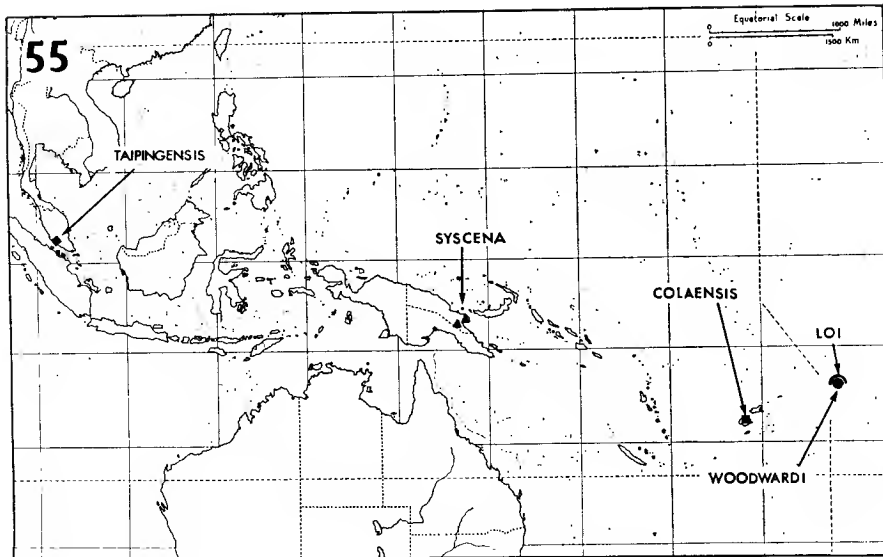


Fig. 55. Group of *Ponera taipingensis*. Distribution.

DISTRIBUTION. Known only from the holotype (MCZ coll.): HONG KONG (Silvestri) —no further data given.

RELATIONSHIPS. See above under species group diagnosis.

Ponera taipingensis Group

The following 5 species form a well circumscribed group, distributed as shown in fig. 55. The first 4—*taipingensis* (Malaya), *syscena* (New Guinea), *colaensis* (Fiji) and *loi* (Samoa) are apparently a closely related series, referred to here as the “*taipingensis* complex”, the 5th species, *P. woodwardi* (Samoa) is evidently a specialized peripheral offshoot of this group.

Workers of the “*taipingensis* complex” are of about the same size as those of the *sinensis* group (head width 0.48–0.56 mm), but differ from them in having proportionately narrow crania (cephalic index 79–86) and in reduction of the mesometanotal suture on the mesosomal dorsum; it may be totally lacking, or represented by a shallow transverse depression, or it may be marked by a finely incised, but very weak line. A distinct clypeal denticle may be developed or it may be represented by a low tumosity. The eyes are small, with 1 to 6 facets, and the apices of the scapes are approximately contiguous with the median occipital border or fall slightly short of it.

P. woodwardi workers resemble the other species in postcephalic structure. However, the head is narrower (cephalic index 77–81) and the scapes longer (scape index 98–102), clearly exceeding the occipital border. The eyes are apparently secondarily enlarged and have 5 to 8 facets.

The known sexuals are normal for the genus, with wing venation of the *coarctata* type. The larvae have 3 pairs of glutinous tubercles on the abdominal dorsum, and the pupae, where known, have cocoons.

The *taipingensis* group is probably cognate with the *sinensis* group. Among its species *syscena* and *loi* are closely related, in fact *loi* seems to represent a not-too-divergent derivative from *syscena*-like stock. *Taipingensis* and *colaensis* are similar, and will probably prove to have close relatives in New Guinea and Indonesia. *P. woodwardi* may have been derived from stock much like *colaensis*.

11. *Ponera taipingensis* Forel Figs. 43-45, 55.

Ponera taipingensis Forel, 1913, Zool. Jahrb. Syst. 36: 12, worker. Type locality: Maxwell's Hill, near Taiping, Malaya (Syntypes examined—Forel coll.).

DIAGNOSIS. Known only from Malaya. The nominate species of the *P. taipingensis* group. Workers differ from those of the related *P. syscena* and *P. colaensis* in possessing a distinct median clypeal tooth. Additionally *colaensis* has a narrower head (cephalic index 81-83 as opposed to 84-86 in *taipingensis*), and wider petiolar node (petiolar node index 88-91 against 84-85); and *syscena* has a much narrower node (PNI 79-82). The 4th member of its complex, *P. loi*, has a distinct clypeal tooth, but the cephalic and petiolar node indices have quite different ranges from those of *taipingensis* (CI 79-83, PNI 78-82), and the ranges of petiole height measurements differ between the 2 species (PH 0.39-0.44 mm in *loi*, 0.45-0.47 mm in *taipingensis*).

This species is distinguished from the only other known Malayan *Ponera* (*P. japonica*) by its larger size (HW 0.52-0.54 mm against 0.43 mm), longer scapes—those of Malayan *japonica* specimens clearly fail to attain the occipital border which is reached by the scapes in *taipingensis*—and thicker petiolar node, forming an almost exact half-circle in dorsal view.

Syntype workers. The following notes are based on 2 syntype workers kindly loaned from the Forel collection by Dr C. Besuchet. One of these is here designated as *lectotype* and has been so labeled. Dimensions (lectotype cited first): HL 0.64 mm, 0.60 mm; HW 0.54 mm, 0.52 mm; SL 0.47 mm, 0.45 mm; CI 84, 86; SI 87; PW 0.45 mm, 0.41 mm; PNL 0.23 mm, 0.21 mm; PH 0.47 mm, 0.45 mm; DPW 0.38 mm, 0.35 mm; PNI 84, 85. General features as in fig. 43-45. Mandibles with 3 large teeth occupying slightly less than apical 1/2 of masticatory border, followed by a series of 5 to 7 small regular denticles. Median clypeal tooth well developed. Eyes apparently 1-faceted, situated about 0.77× distance from lateral occipital border to midpoint of anterior genal border. Scapes almost exactly reaching median occipital border when laid back along head. Funiculus incrassate but lacking a segmentally differentiated club; apical antennomere about as long as 2 preceding together. General form of mesosoma much as in *P. scabra*, mesometanotal suture not distinctly incised dorsally, but represented by a shallow broad transverse convexity. Lateral mesonotal suture almost obliterated. Posterolateral angles of propodeum each marked by a slightly raised carina, forming angles of a little less than 90° when viewed from above. Lateral and declivitous faces of propodeum, viewed from same aspect, almost straight, sides converging slightly anteriorly. Petiolar node as in figs. 44 and 45. Dorsal face, viewed from above forming an almost exact half-circle; posterior border very slightly sinuate, feebly convex in middle, and weakly concave at sides.

Mandibles smooth and shining, clypeus irregularly shagreened, moderately shining. Head opaque, closely covered with moderately large, almost contiguous, punctae, about 0.01 mm in diameter. Occipital area shining, with scattered small punctures. Pronotum moderately

shining, finely and closely punctate. Mesonotum with puncturation similar to that of head, but a little more scattered; dorsum of propodeum similarly, but more sparsely punctate—the inter-punctural intervals slightly more than average diameter of punctae. Sides of mesosoma moderately punctate and feebly shining, a little more so on middle of lateral faces of pronotum and propodeum. A somewhat effaced longitudinal striate-rugosity on lower 1/2 of mesepisternum and on metepisternal area. Declivitous face of propodeum shining, with traces of an effaced transverse rugosity, much as described above for *P. chapmani*. Sculpture of node and gaster as in *chapmani*, the almost vertical striation of the posteroventral parts of the sides of the node less distinct, and the punctae of the 1st 2 gastric tergites smaller.

Pilosity sparse, limited to a few fine erect to suberect hairs on mandibles, clypeus, frontal lobes, dorsa of mesosoma and node and entire gaster, where they are relatively very sparse. Pubescence everywhere moderately abundant. Color as described above for *P. chapmani*.

Immature stages and sexuals unknown.

DISTRIBUTION. Known only from the type material. MALAYA: Maxwell's Hill, near Taiping, 1200 m, 2 workers collected from a rotting branch (Buttle-Reepen) Forel collection.

RELATIONSHIPS. See above under species group diagnosis.

12. *Ponera syscena* Wilson Figs. 46-48.

Ponera syscena Wilson, 1957, Bull. Mus. Comp. Zool. **116** (6): 384, worker. Type locality: between Yunzain and Joangeneg, Huon Peninsula, NE New Guinea. (holotype examined—MCZ.); 1958, Bull. Mus. Comp. Zool. **119**(4): 340.

DIAGNOSIS. A member of the *P. taipingensis* group, close in size (*i.e.*, HW) to the Malayan *P. taipingensis*, and the Fijian *P. colaensis* but readily distinguished from them by the narrower petiolar node (PNI 79-82 mm as opposed to 84-91 mm in these other species). The Samoan *P. loi* is similar to this species; the characters distinguishing the two are discussed below under *P. loi*.

Additional description. The following notes are based on Wilson's unique holotype and a series of 7 additional workers from the vicinity of Wau, NE New Guinea.

1. Dimensions (holotype cited first): HL 0.61 mm, 0.60-0.62 mm; HW 0.50 mm, 0.48-0.50 mm; SL 0.44 mm, 0.44-0.46 mm; CI 84, 80-82; SI 86, 90-92; PW 0.39 mm, 0.39-0.40 mm; PNL 0.22 mm, 0.21-0.22 mm; PH 0.40 mm, 0.39-0.42 mm; DPW 0.31 mm, 0.31-0.33 mm; PNI 79, 80-82. The discrepancies in CI and SI of the holotype are due to its having a slightly greater head width measurement than would be expected; in every other regard it agrees with the other specimens exactly. Wilson's diagnosis adequately characterizes this species. The following diagnostic notes should allow verification of specimens running to *syscena* in the key above.

2. The clypeus of the holotype is not distinctly dentate, but bears a low raised blunt tumosity, which is clearly a vestigial tooth. One of the Wau specimens has a similar clypeus, but the others each have a moderately acute clypeal tooth, almost 0.02 mm high and a little wider at its base.

3. The scapes almost exactly reach median occipital border when laid back on head. Funiculus as in *P. clavicornis*—effectively lacking a differentiated club, but in some specimens the apical 4 or 5 segments form a very feeble club.

4. Eyes with 3 to 6 very indistinct facets, situated about 0.82 to $0.87\times$ the distance from lateral occipital border to midpoint of anterior genal border.

5. Palpal formula: *Maxillary 2: Labial 2* (one specimen dissected).

6. Mesometanotal suture completely lacking on mesosomal dorsum.

♀, ♂ and immature stages unknown.

DISTRIBUTION AND MATERIAL EXAMINED. NE NEW GUINEA: Native trail between Yunzain and Joangeng, Mongi Watershed, Huon Peninsula, 1300 m, midmountain rain forest, 7.IV.1955 (E. O. Wilson)—holotype (MCZ). Kunai Creek, near Wau, 1500 m, strays ex rotting wood fragment, and under moss on log, damp rain forest gully, VI.1962 (RWT accs. 1956, 1984).

The holotype and additional workers are in the MCZ collection, duplicate specimens in BISHOP, BMNH, and CSIRO.

RELATIONSIPS. See above under species group diagnosis.

13. *Ponera colaensis* Mann Figs. 49–51.

Ponera colaensis Mann, 1921, Bull. Mus. Comp. Zool. **64** (5): 417, worker. Type locality: Waiyanitu, Viti Levu, Fiji Is. (holotype examined—USNM).—Santschi, 1928, Rev. Suisse. Zool. **35**, 68, distribution.—Wilson, 1959, Bull. Mus. Comp. Zool. **119** (4): 343, distribution.

DIAGNOSIS. A species apparently endemic to the Fiji Is. (Viti Levu and Lau group). One of the larger members of the *P. taipingensis* group; somewhat similar to the Malayan *P. taipingensis*, but distinguished from it by the narrower head and wider petiolar node (cephalic index 81–83, petiolar node index 88–91 as opposed to 84–86 and 84–85 respectively in *taipingensis*). *P. syscena* (New Guinea) and *P. loi* (Samoa) are both similar to *colaensis*, but they have much narrower petiolar nodes (PNI 79–82 in *syscena*, 78–82 in *loi*).

P. colaensis is the only known Fijian *Ponera* species lacking an incised dorsal mesometanotal suture. The other Fijian species are all smaller, except for the slightly larger *P. manni* (HW 0.57 mm in the unique holotype), which has a much narrower petiolar node (PNI 73 opposed to 88–91 in *colaensis*).

The unique known ♀ of *colaensis* differs from those of the related *P. loi* by her smaller size, longer scapes, and broader petiolar node (HW 0.54 mm; SI 91; PNI 82, opposed to 0.60–0.63 mm; 83–87, and 75–76 respectively in *P. loi*).

Additional Description.

Worker. The following dimensions are those of the holotype (USNM) and a single worker (MCZ) with labels identical to those of the holotype. This latter specimen was apparently overlooked by Mann at the time of description of the species. HL 0.62 mm, 0.61 mm; HW 0.50 mm; SL 0.45 mm; CI 81, 82; SI 90; PW 0.42 mm, 0.40 mm; PNL 0.20 mm; PH 0.43 mm; DPW 0.37 mm, 0.36 mm; PNI 88, 90.

Thirty additional workers I collected at Nandarivatu, Viti Levu, have the following measurements and indices: HL 0.62–0.65 mm; HW 0.50–0.54 mm; SL 0.46–0.49 mm; CI 81–83; SI 88–92; PW 0.41–0.44 mm; PNL 0.20–0.22 mm; PH 0.41–0.43 mm; DPW 0.36–0.38 mm; PNI 88–91.

Mann's diagnosis is generally adequate, but the following additional notes are pertinent:

1. Clypeus with vestigial median anterior tooth, in the form of a bluntly pointed low tumosity.

2. Palpal formula: *Maxillary 2; Labial 2* (3 Nandarivatu specimens dissected).

3. Eyes with maximum diameter ranging from 0.02 mm to almost 0.04 mm, with 3–5 rather indistinct facets; their anterior borders situated about 0.87× the distance from lateral occipital border to midpoint of anterior genal border.

4. Scares almost exactly attaining median occipital border—in smaller specimens they may fail to do so by a very slight margin (less than 1/4 their maximum thickness).

5. Dorsal mesometanotal suture never distinctly incised, although in several specimens it is represented by a shallow broad transverse impression. Lateral mesonotal suture distinctly marked. Sides and declivitous face of propodeum almost straight in dorsal view. Posterolateral corners of propodeum slightly raised, forming angles of about 90° when viewed from above.

6. Erect to sub-erect pilosity sparse on mandibles, clypeus, frontal lobes, dorsa of mesosoma and node, and entire gaster; more sparse on front of head and more abundant on gaster. Distinct whitish adpressed pubescence everywhere abundant.

7. The holotype and Mann's Waiyanitu specimen are rich medium reddish brown in color. They may possibly have been semi-callow when taken, or else affected by preservation, as the remaining material is darker. The Nandarivatu examples are uniformly very dark reddish brown, with mandibles, antennae, legs, and gastric apex a bright rich yellowish brown.

♀. A single alate specimen collected with workers at Nandarivatu (my accession no. 35) has the following characters: HL 0.65 mm; HW 0.54 mm; SL 0.49 mm; CI 83; SI 91; PW 0.49 mm; PNL 0.22 mm; PH 0.47 mm; DPW 0.40 mm; PNI 82; maximum diameter of eye 0.18 mm; ocular index 33. Conforming to the general plan of ♀ structure for the genus. Wing venation of the *P. coarctata* type. Differing from the workers in the usual characters of full sexuality, and agreeing with them in color, sculpturation and pilosity. The median clypeal denticle is reduced to an indistinct low tumosity as in the workers. When laid back along the head the scapes almost exactly reach the median occipital border.

♂ and larva unknown; pupae of all castes enclosed in cocoons.

DISTRIBUTION AND MATERIAL EXAMINED. The only *colaensis* examined were from Viti Levu; Santschi's published records (1928) have not been verified. FIJI IS.: *Viti Levu*: Nandarivatu, 15–19.II.1962 (RWT, accs. 29, 35, 82, 83). Waiyanitu (W. M. Mann) holotype USNM, additional specimen MCZ. *Lau Group*: Kambara (Santschi 1928).

ECOLOGY. My collections were made in disturbed rain forest in the Nandarivatu Forestry Nature Preserve at 840 m, and from relatively undisturbed forest on the slopes of Mt Lomolaki, at about 900 m. The majority of the specimens were taken from Berlese funnel samples of leafmold, moss off rotting logs, or debris from a tree fern stump. Accession No.

29 consisted of several workers taken with pupae under spongy moss covered bark on a rotting log.

RELATIONSHIPS. See above under species group.

14. ***Ponera loi*** Taylor, new species Figs. 52-55.

DIAGNOSIS. Known only from the Samoan island of Upolu. Similar to the New Guinean *P. syscena*, particularly in having a relatively narrow petiole node (petiolar node index 78-82). This character allows immediate separation of *syscena* and *loi* from the other members of the *taipingensis* complex, whose PNI's range from 84-91.

Characters distinguishing *syscena* from *loi* are given below in the description of *loi*. These 2 species are closely related, in fact *loi* is probably derived from stock close to, or conspecific with, *syscena*.

Workers of *P. loi* are easily distinguished from the sympatric *P. woodwardi* by differences in scape index (84-91 in *loi*, 98-102 in *woodwardi*). The other sympatric species on Samoa (*incerta*, *swezeyi* and *tenuis*) are all considerably smaller.

The ♂ and ♀ of *syscena* and the ♂ of *loi* are not known. Characters separating *loi* ♀♀ from those of *woodwardi* and *colaensis* are given following the ♀ description below.

Worker. (Based on the holotype and 8 paratypes collected at Afiamalu by Zimmerman in 1940 and by Ettershank and me in 1962). Dimensions (holotype cited first): HL 0.66 mm, 0.62-0.70 mm; HW 0.53 mm, 0.51-0.58 mm; SL 0.46 mm, 0.44-0.52 mm; CI 80, 79-83; SI 87, 84-91, PW 0.40 mm, 0.37-0.42 mm; PNL 0.21 mm, 0.20-0.23 mm; PH 0.41 mm, 0.39-0.44 mm; DPW 0.33 mm, 0.30-0.34 mm; PNI 82, 78-81. With the characters of the *P. taipingensis* species group as defined above. Close to *syscena* in the details of mandibular, clypeal, and antennal structure, and in color, sculpturation, pubescence and pilosity. The *loi* types differ from the available *syscena* material in the following characters:

1. Head length 0.62-0.70 mm as opposed to 0.60-0.62 mm in *syscena*. The frequency distribution of HL measurements in *loi* is strongly skewed toward the high values. The mean HL values of the 2 species are: *loi* 0.66 mm (N=9); *syscena* 0.61 mm (N=7).

2. Head width 0.51-0.58 mm, opposed to 0.48-0.51 mm in *syscena*. The mean values again give more conclusive separation—in *loi* the mean HW is 0.54 mm (N=9); in *syscena* it is 0.49 mm (N=7).

3. The head of *P. loi* is proportionately larger relative to the body than that of *syscena*. In the former the head width ranges from 1.31 to 1.38× the pronotal width, while in the latter, values of 1.23-1.28× are yielded.

4. Median clypeal denticle distinctly developed in *loi*, vestigial in *syscena*.

5. The outline of the mesosomal dorsum in *loi* (fig. 53) is slightly indented at the mesometanotal suture, where it is straight and uninterrupted in *syscena*. The mesometanotal suture of *loi*, unlike that of *syscena*, is represented by a fairly marked transverse impression, which is accompanied by a fine and indistinct incised sutural trace in some specimens.

♀. 3 dealate paratypes collected by Swezey and Zimmerman in 1940 have the following dimensions: HL 0.71-0.73 mm; HW 0.60-0.63 mm; SL 0.50-0.55 mm; CI 85-86; SI 83-87; PW 0.50-0.53 mm; PNL 0.21-0.23 mm; PH 0.46-0.50 mm; DPW 0.38-0.40 mm; PNI 75-76; maximum diameter of eye 0.20; ocular index 32-33. Conforming to the general plan of

♀ structure for the genus, and differing from the workers in the usual characters of full sexuality. Medium clypeal denticle distinctly developed, as in the worker, and the apices of the scapes are almost exactly contiguous with the median occipital border.

Females of *loi* are distinguished from related species by the same characters differentiating the workers. The unique known *P. colaensis* ♀ is smaller, with a proportionately wide petiolar node (HW 0.54 mm; PNI 82), and *woodwardi* ♀♀ have narrower heads and longer scapes (CI 80-84; SI 99-102).

MATERIAL EXAMINED. SAMOA: *Upolu*: Afiamalu (Type Locality), 6 paratype workers and a ♀ collected by beating at elevations ranging from 640 to 670 m by E. C. Zimmerman on the following dates in 1940: 6, 11, 19 (♀), 30.VI. 5, 11.VII; a single paratype worker, ex dead log, 660 m, 10.VI.1940 (O. H. Swezey); a single worker (Holotype) ex moss on log, disturbed rain forest, 700 m, 30.III.1962 (R. W. Taylor acc. 632); 2 paratype workers, ex separate Berlese funnel samples of moss off logs, disturbed forest, 700 m, IV. 1962 (G. Ettershank accs. 8, 37). Malololelei Road, 1 paratype ♀, beating shrubbery, 485-545 m, 8.VII.1940 (E. C. Zimmerman).

TYPES. Holotype and paratypes (worker and ♀) in MCZ collection. Paratypes in BISHOP, BMNH, CSIRO, Forel Coll. and USNM.

ECOLOGY AND DISTRIBUTION. *Ponera loi* is known only from forested areas near Afiamalu. According to Zimmerman (pers. comm.), his specimens were taken in undisturbed forest, at roadsides or along native trails. The Taylor and Ettershank material is from the disturbed forest area at Afiamalu discussed below under *P. incerta*. *P. loi* is evidently a rather rare species and appears, from the Taylor and Ettershank collections, to be much less abundant at Afiamalu than the similar and sympatric *P. woodwardi*. In intensive collecting there I took it only once, although it may have been overlooked at times, due to my confusing it with the common *woodwardi*, which was not always collected.

A rough quantitative estimate of the relative abundance of the two species in 1962 can be obtained from Ettershank's Berlese funnel material. He processed 31 samples of moss collected at Afiamalu during April. Seventeen of these were from the ground or fallen logs, and 14 were from the trunks or branches of standing trees. *P. woodwardi* was present in 7 ground layer samples, and 2 tree moss ones, while *P. loi* occurred only in 2 ground moss berlesates. In the ground layer samples containing these species the frequency of *loi*, relative to *woodwardi*, was thus 0.29, and in all samples it was 0.17.

It is of interest to compare this value with that of Zimmerman's collections, made 22 years previously. All of his material was taken by sweeping or beating, and each specimen represents a separate collection. He took 6 workers and 3 dealate ♀♀ of *loi*, and a single dealate ♀ of *woodwardi*; thus the frequency of *P. loi* in his collections was 0.90.

Comparison of these values for 1962 and 1940 collections, and consideration of the factors which might explain the differences between them is fraught with difficulty. For example, the Ettershank material was collected in a disturbed area where apparent irruption of many native and introduced ant species was observed, while Zimmerman collected in less disturbed forest, presumably with a more normally balanced fauna. It may be that *woodwardi* had responded more vigorously to ecological release in the disturbed forest than had *loi*, thus distorting their true relative abundance in Samoan forests. We know nothing of the biology of *P. loi*, and it may be that differences in technique employed by the two collec-

tors, along with biological differences between the two species, has occasioned the discrepancies.

In spite of these difficulties *P. loi* appears to have diminished in abundance relative to *P. woodwardi* since 1940. Until it is proved that the available data are false this situation deserves consideration. It is suggested that active competition has taken place between the two species and that this has occasioned the change in their relative frequencies, *woodwardi* having become increasingly abundant at the expense of *loi*. If this supposition should be true it would hold considerable zoogeographic interest.

It is now known from extensive studies on the Polynesian ants by E. O. Wilson and myself that the more dominant tramp species of Formicidae in such genera as *Pheidole* and *Solenopsis* may completely replace one another on individual Pacific Islands, and may show mutually exclusive distributional patterns suggesting that they competitively exclude one another.

It is clear from the Polynesian studies that individual island faunas are very dynamic, with periodic cycles of extinction and competitive replacement, at least among the tramp ant species. The possibility that a similar competitive interchange in relative abundance may have taken place between the comparatively scarce cryptobiotic forest *Ponera* species under discussion is of considerable interest. Future collectors on Upolu should keep this problem in mind, for strategic collecting may clarify the relationships between these two species, and could determine whether the apparent faunal change is biologically meaningful.

RELATIONSHIPS. It would be interesting to know the real status of *loi* and *woodwardi* as members of the Samoan fauna—i.e., whether they are autochthonous endemics, or widespread indigenous species, or human introductions. Both species appear to be descended from *syscena*-like stock and *woodwardi* is presumably the more derived. Apart from this, and the observation that they are probably not directly cognate, little more can be said on this point.

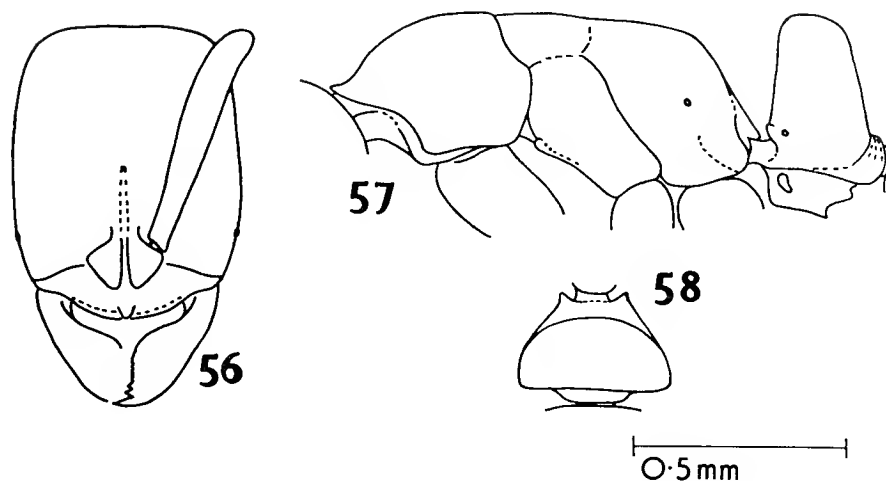
15. *Ponera woodwardi* Taylor, new species Figs. 7, 55-58.

DIAGNOSIS. Known only from the mountains of central Upolu, Samoan Is. The worker is unique among the medium sized *Ponera* (those with HW 0.43-0.60 mm) by virtue of its relatively narrow head (CI 76-81) and long scapes, which clearly exceed the occipital border, and yield scape index values of 98-102. No cephalic index value less than 80 is known in any other medium sized *Ponera*, and only one other species, *P. loi*, has a CI range extending below 80. All other species of *Ponera* with scapes exceeding the occipital border have cephalic index values higher than 88, and the next lowest scape index value in the whole genus is 95.

Additional diagnostic features include the size (HW 0.53-0.60), the presence of a distinct median clypeal tooth, the somewhat enlarged eyes and the tendency for reduction of the mesometanotal suture.

P. woodwardi ♀♀, like the workers, are characterized by their narrow heads, and relatively long scapes.

P. woodwardi is easily distinguished from most of the other Samoan *Ponera* species by its considerably larger size and dark coloration. *P. loi* has approximately the same head width as *woodwardi* but the head is broader, and the scape index lower.



Figs. 56-58. *Ponera woodwardi* n. sp., worker (Holotype): 56, head; 57, mesosoma and node; 58, node, dorsal view.

Holotype worker. HW 0.55 mm; HL 0.73 mm; SL 0.56 mm; CI 76; SI 102; PW 0.44 mm; WL 0.97 mm; PH 0.50 mm; PNL 0.25 mm; DPW 0.37 mm; PNI 84. Mandibles with 3 well developed teeth occupying approximately apical 2/5 of masticatory border; remainder of border with 6 or 7 irregular, medium sized denticles. Eyes moderately well developed, indistinctly 7-faceted, their diameter about 0.05 mm. Anterior border of eye located approximately $0.93\times$ the distance from lateral occipital border to midpoint of anterior genal border. Scapes exceeding occipital border by slightly less than their maximum thickness. Funiculus lacking a segmentally differentiated club. Anterior face of clypeus with a distinct, moderately acute, median tooth, about 2/3 as high as its width at base. Palpal formula: *Maxillary 2; Labial 2* (inspected). Mesometanotal suture not present as a sharply incised line breaking sculpture, but represented by a fairly distinct, narrow, shallow indentation traversing mesosomal dorsum. Posterolateral margins of propodeum fairly narrowly rounded, forming angles of about 90° , viewed from above.

Petiolar node, in side view, massive, sub-rectangular, tapering only slightly dorsally. Dorsal surface, viewed from above, forming slightly less than a half-circle; posterior face feebly concave; posteroventral angle fairly obtuse; fenestra elliptical, small but distinct.

Mandibles and clypeus smooth and shining. Cephalic dorsum densely punctate, opaque to sub-opaque; sides of head less densely punctate, punctures smaller and surface feebly shining. Dorsum of alitrunk moderately shining, less densely punctured than head. Punctures of pronotum and propodeum finer and more spaced than those of mesonotum; those of propodeum most diffuse. Sides of alitrunk shining, with a few scattered point-punctures. Lower aspects of mesepisterna and lateral propodeal faces with a few very fine, partly indistinct, longitudinal striae. Petiole largely smooth and shining with a few scattered punctures laterally and dorsally. Postpetiole and gaster moderately punctate, their surfaces fairly shiny; sculptural intensity diminishing posteriorly.

Moderately long erect yellowish hairs present on mandibles, clypeus, postgenae, dorsum of node, lower edge of subpetiolar process, and entire gastric surfaces. Those on gastric

apex longer and coarser. A few short fine erect hairs on scapes and anterior pronotal dorsum. Pubescence adpressed, abundant on head, antennae, mesosomal dorsum and gaster. Less abundant on sides of mesosoma.

Mandibles, clypeus, frontal lobes, antennae, and legs medium yellowish brown. Head and body largely very dark brown, with a reddish brown cast on neck and edges of pronotum, lower aspects of mesepisterna and lateral and declivitous faces of propodeum, sides of petiole, subpetiolar process, ventral and apical parts of gaster, and posterior parts of its tergites.

TYPE LOCALITY. Afiamalu, 700 m, Upolu, Western Samoa, 10. III. 1962 (R. W. Taylor). Holotype selected from a series of individuals taken nesting in a small fragment of rotting wood on floor of disturbed rain forest.

Paratype workers. 35 paratype workers from various collections made at Afiamalu between 1940 and 1962 (see below under "Material Examined") have the following dimensions and indices: HL 0.69–0.75 mm; HW 0.53–0.60 mm; SL 0.55–0.60 mm; CI 77–81; SI 98–102; PW 0.44–0.48 mm; PNL 0.23–0.25 mm; PH 0.48–0.53 mm; DPW 0.35–0.39 mm; PNI 78–84. The specimens agree well with the holotype in general structure. Number of posterior mandibular denticles varies from 5 to 7. Eyes vary in diameter from about 0.04 mm to slightly less than 0.06 mm, with 5 to 8 moderately distinct facets; scapes always clearly exceed median occipital border by a distance of up to slightly more than $\frac{2}{3}$ their maximum thickness.

The degree of impression of the mesometanotal suture varies. Minimally developed, it is a broad shallow impression crossing the dorsum of the mesosoma. In most specimens this is fairly narrow and distinct, and even with strongly reflected light, no sharply incised sutural trace is visible. Some examples, however, have a fine incised suture, readily visible in reflected light.

The tendency for parts of the body to be lightly infuscated, relative to the general coloration, seems to be common in this species. In some specimens the extent of lighter areas is greater than that described for the holotype, while others are almost uniformly dark brown; *woodwardi* is evidently slow in developing full adult coloration following emergence.

Paratype ♀♀. (Based on 3♀♀, an alate and 2 dealates, collected at Afiamalu and Malolelei by Woodward, I. 1956.) HL 0.73–0.75 mm; HW 0.60–0.61 mm; SL 0.60–0.61 mm; CI 80–84; SI 99–102; PW 0.52–0.55 mm; DPW 0.37–0.40 mm; PNL 0.24–0.26 mm; PH 0.54–0.55 mm; PNI 71–73; maximum diameter of eye 0.20 mm; ocular index 33–34. Differing from the worker in the usual characters of full sexuality and conforming to the basic plan of ♀ structure in *Ponera*. Wing venation of *coarctata* type as in fig. 7.

Paratype ♂♂. (Based on 2♂♂ collected with the holotype nest series.) HL 0.55 mm; HW (across eyes) 0.53 mm; CI 96; WL 1.08 mm; PNL 0.22 mm; PH 0.32 mm; DPW 0.22 mm; maximum diameter of eye 0.27 mm; ocular index 51; palpal formula (1 specimen dissected): *Maxillary* 2: *Labial* 2, as in the ♀ castes. Conforming to the general structural plan of *P. pennsylvanica*, as described above. Wing venation as in ♀. Structure of terminalia of the same basic pattern as in *P. pennsylvanica*; pygidial spine relatively strong; dorsal process of paramere broader and less digitate, lacking thickened struts along its edges.

Head and mesosoma very dark blackish brown, metasoma slightly paler; antennae, legs,

wing veins, and genitalia paler—dull medium brown. The ♂ of *P. woodwardi* has a relatively low cephalic index value compared with other similar sized *Ponera*, known males of which all have CI values exceeding 100.

Immature stages. Larvae from the holotype nest are similar to those of *P. alpha* in possessing 3 pairs of dorsal abdominal "door knob" tubercles.

The pupae of all castes are enclosed in cocoons.

DEPOSITION OF TYPE MATERIAL. Holotype worker and paratypes of all castes in MCZ collection. Paratypes, including ♂♂ and ♀♀, in BISHOP, BMNH and CSIRO. Worker paratypes in the following collections: AMNH; Australian Museum, Sydney; Auckland Institute and Museum, New Zealand; California Academy of Sciences; Emery coll.; Forel coll.; National Museum of Victoria, Australia; Paris Museum; Santschi coll.; USNM; Yasumatsu coll.

MATERIAL EXAMINED. Apart from the holotype, all the specimens listed here have been designated as paratypes. The collectors G. Ettershank, T. E. Woodward and R. W. Taylor are referred to by their initials. Accession numbers following Ettershank or Taylor records refer to material in the MCZ collection. SAMOA: *Upolu*: Afiamalu, 700 m, (*Type locality*) beating, 1 dealate ♀, 30.VI.1940 (E. C. Zimmerman); strays ex soil under stone, disturbed rain forest, 2 workers, 10.III.1962 (RWT acc. 245); nests ex rotting wood fragments (less than 6 cm diameter), rain forest floor, 10. III. 1962 [RWT accs. 253 (*holotype nest series*—10 workers, 6♂♂); 254 (9 workers); 259 (3 workers)]; nest under moss on rotting log, disturbed forest, 1 worker, 30.III.1962 (RWT acc. 632); ground moss berlesate, rain forest, 3 workers and 1 alate ♀, 6.I.1956 (TEW); leafmold berlesate, rain forest, numerous workers, 16.III.1962 (RWT acc. 584); berlesates, moss ex ground and rotting logs, disturbed rain forest, III-IV.1962 (RWT accs. 302, 584, 2315-2319, 2322-2324); tree moss berlesates, disturbed rain forest, 19.I.1956 (TEW); III-IV.1962 (RWT accs. 300 <2 m above ground); 582 (15 m); 580, 581, 2307, 2308 (all at 10 m above ground); GE accs. 37 (at 11 m); 44 (8 m above ground). Malololelei, ca 650 m, ex moss berlesate, rain forest, dealate ♀, 19.I.1956 (TEW).

DISTRIBUTION AND ECOLOGY. The known distribution of *woodwardi*, like that of *P. loi*, is limited to the Afiamalu-Malololelei area at about 650-700 m elevation on Upolu. This distribution is reflected not only in recent collections but also in those dated 1940 and 1956. All of the above collectors worked extensively at a variety of stations at all elevational levels, not only on Upolu but also on Savaii and Tutuila. Notwithstanding, *woodwardi* has not been taken away from Afiamalu.

Where present this species is not uncommon in rain forest. During my Samoan field work I often took strays under moss on logs or standing trees, or in wood fragments lying on the forest floor. Like other Samoan endemics *woodwardi* had apparently undergone ecological release in an area of partly cleared and rather disturbed forest at Afiamalu, and was more abundant there than in the adjacent undisturbed forests. This situation is discussed below under *P. incerta*. Specimens of *woodwardi* were taken in berlesates of tree moss collected as high as 15 m above ground level.

The type colony was in a rotting branch fragment about 35 cm long and 8-10 cm in diameter, lying on the floor of the cleared forest area. The nest was rather diffuse, with adults and brood distributed throughout the more rotted half of the branch, in preformed

crack crevices or beetle galleries. A number of nests were collected under thick moss on the upper surfaces of the many logs lying in the partially cleared forest area ; and sufficient Berlese funnel collections were taken to indicate that nests are commonly found in these situations. Brood, in these cases, was located either in galleries under the moss, against the log surface, or in preformed cavities in the more rotted parts of the wood itself.

Several observation colonies were maintained for periods of 2 to 6 days. Aspects of colony behavior and brood care, including studies on the function of the larval tubercles, were carried out. Unfortunately feeding could not be induced by presentation of numerous small insects and other arthropods. On one occasion I discovered two apparent middens of small (*ca* 10 mm long) diplopods, close to colony nuclei of *woodwardi* nesting under log moss. Similar diplopods were not accepted in observation nests.

The introduced *Hypoponera confinis* (Roger), *New combination*, an ant of similar size and general ecology to *woodwardi*, occurs fairly abundantly at lower elevations on Upolu, where *woodwardi* is apparently absent. *H. confinis* was not encountered at Afiamalu by me but a specimen was collected by Zimmerman in 1940. While in Samoa I gained the distinct impression that the niche-equivalent of *confinis* at low elevations was occupied by *woodwardi* at Afiamalu, and consider it possible that *woodwardi* has contracted its range to higher elevations, through competitive inferiority to *confinis* in lowland areas. If this impression is correct the outcome of a competitive situation involving these two species may be influenced by ecological factors associated with elevational change, or with the degree of human disturbance in the environment. *H. confinis* is a fairly widespread tramp species, ranging at least from India and Ceylon through Melanesia and Polynesia to the Society Islands. It seems to have a capacity for survival in disturbed situation ; a capacity perhaps less developed in *woodwardi*.

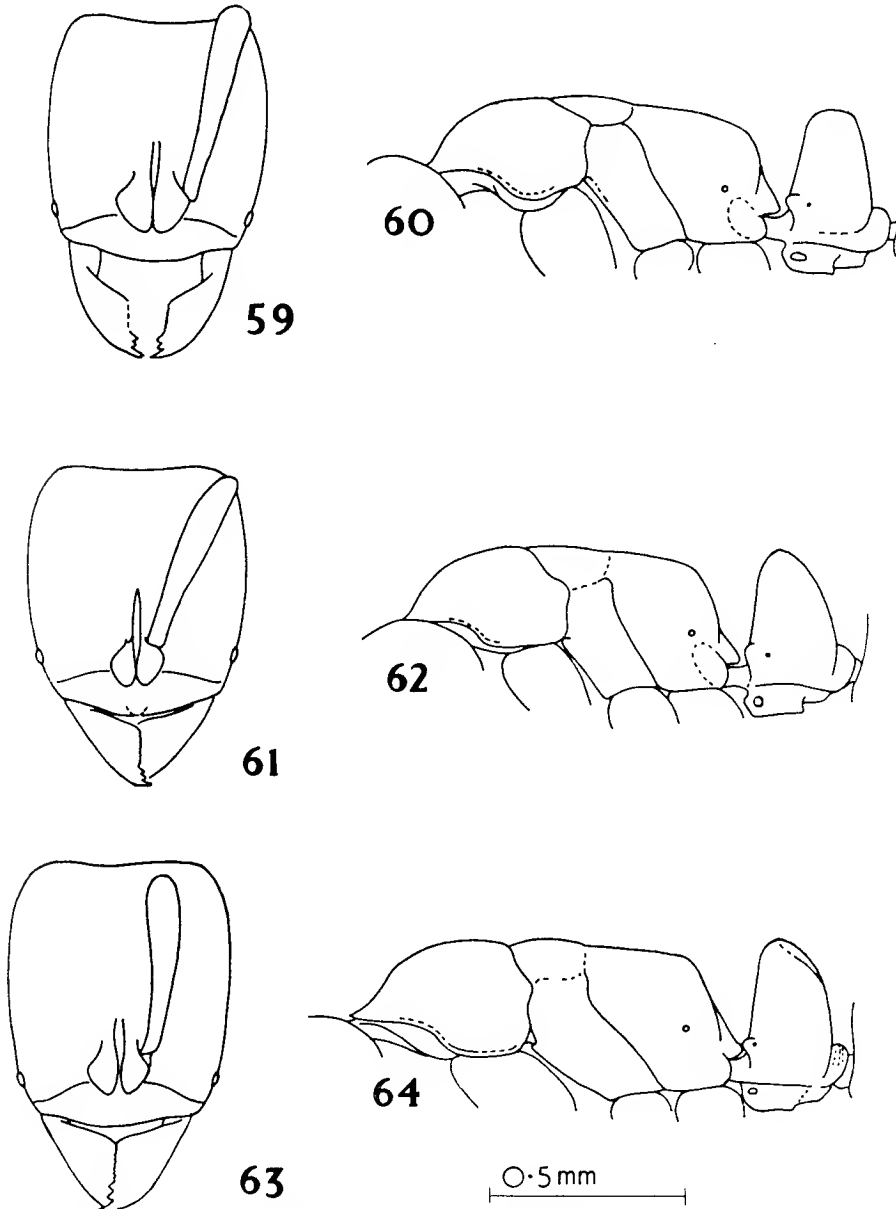
RELATIONSHIPS. *P. woodwardi* is related to the Fijian *P. colaensis*. It is clear that our knowledge of the Fijian *Ponera* fauna is very deficient and it may be that Fijian species closer to *woodwardi* may be eventually unearthed there. Indeed it is possible that *woodwardi* itself is a native Fijian species introduced secondarily into Samoa.

Ponera elegantula Group

The following 3 species, *P. augusta* (New Guinea), *P. borneensis* (Borneo), and *P. elegantula* (New Guinea), have been grouped together mainly because they all have distinctly larger, more highly faceted eyes than those of any other *Ponera* species. The compound eyes of the available worker specimens have 9 to 16 facets, whereas all other known species of the genus have less than 6 (except *P. woodwardi* of Samoa which has secondarily enlarged eyes with 7 to 11 facets). Additional points of resemblance are less easily described and involve general habitus. The 3 species are similar, and resemble the members of the *sinensis* and *taipingensis* groups. Detailed examination of more specific characters such as the cephalic index, the relative length of the scapes, the nature of the worker mesometanotal suture and details of sculpturation and pubescence, show them to vary considerably, as discussed below under *elegantula*. Indeed variation in these features almost covers the whole range of complexity seen in the *sinensis* and *taipingensis* groups.

I may be in error in classifying these species together, as a supposed natural group. In so doing it has been assumed that they represent a line derived from rather primitive stock,

of about the *selenophora* grade, in which the eyes have been secondarily enlarged, and other characters have evolved in parallel to the genus-at-large. These species could represent 3



Figs. 59-64. Group of *Ponera elegantula*. *Ponera augusta* n. sp., worker (Holotype): 59, head; 60, mesosoma and node. *Ponera borneensis* n. sp., worker (Holotype): 61, head; 62, mesosoma and node. *Ponera elegantula* Wilson, worker (Holotype): 63, head; 64, mesosoma and node.

separately derived large-eyed forms, rather than a single lineage. At present only a subjective decision can be made, and I have weighed the large-eyed character heavily in grouping them together.

If this interpretation is correct the group shows a fine morphoclinal succession, with *augusta* at the primitive extreme, and *elegantula* at the derived end (see discussion below under *P. elegantula*).

16. ***Ponera augusta*** Taylor, new species Figs. 35, 59, 60.

DIAGNOSIS. Known only from the eastern highlands of New Guinea. Easily distinguished from other *Ponera* species of similar size by the following set of characters:

1. Large eyes with 11 to 15 facets.
2. Broad head (cephalic index 90-93).
3. Long scapes, which clearly exceed the occipital border by a distance almost equal to their maximum thickness.
4. Coarsely punctate-opaque sculpturing on genae and on mesosomal dorsum.
5. Mesometanotal suture distinctly incised.

Holotype worker. HL 0.62 mm; HW 0.57 mm; SL 0.51 mm; CI 92; SI 89; PW 0.44 mm; PNL 0.22 mm; PH 0.43 mm; DPW 0.36 mm; PNI 82. General structure as shown in accompanying figures. Apical 1/2 of masticatory mandibular border with 3 strong teeth, remaining border with a series of 8 or 9 minute, irregular denticles. Clypeus slightly produced in center, but not dentate. Eyes relatively large, maximum diameter approximately 0.06 mm, composed of about 11 or 12 indistinct facets; situated about $0.93\times$ the distance from lateral occipital border to midpoint of anterior genal border. Scapes surpassing median occipital border by about 3/4 their maximum thickness. No antennal club differentiated, but funicular apex incrassate; apical antennomere about as long as the 2 preceding together.

Dorsal mesometanotal and lateral mesonotal sutures sharply incised. Posterolateral propodeal edges raised, forming angles of about 80° , viewed from above. Node, from above, transverse, dorsal face forming much less than a half-circle, posterior border almost straight. Petiolar profile as in figure 60. Subpetiolar process low, fenestra small but distinct; posterolateral teeth obtuse, weakly developed.

Mandibles smooth and shining; front and sides of head and clypeus opaque, closely and coarsely punctate, the punctures almost contiguous, about 0.008 mm in diameter; scapes coarsely shagreened. Entire dorsal and lateral faces of mesosoma subopaque, coarsely and closely punctate; puncturation of sides of propodeum partly effaced. Punctures of pronotal dorsum about 0.008 mm in diameter, separated by distances about equal to 1/2 their maximum diameter. Mesonotal and propodeal punctures slightly larger and more dense; those of mesonotum more closely spaced than elsewhere on mesosoma but not as close as in *P. alpha*. Puncturation of sides of mesosoma finer and less dense than on dorsum, mesepisternum sub-opaque with a dense cover of irregular large punctures, especially on its lower 1/2, striation of metepisternal area indistinct, almost vestigial. Propodeal declivity strongly shining, with microsculpture as described above for *P. alpha*. Posterior face of node smooth and shining, its remaining surfaces, and gaster, moderately shining, with a close cover of fairly large pilosity-bearing punctures, less distinctly impressed than those of mesosoma.

Short erect to sub-erect pilosity sparse on mandibles, scapes, head and mesosomal dorsum; more abundant on clypeus, apex of node, subpetiolar process, and gaster, where the apical and ventral hairs are longest. Moderately dense, fine white pubescence everywhere abundant.

Color dark brown, almost black; subpetiolar process and apex of gaster infuscated yellowish brown. Scapes dull medium yellowish brown; mandibles and legs bright medium yellowish brown.

Paratype workers. 5 paratype workers from the same berlesate as the holotype have the following dimensions: HL 0.60–0.61 mm; HW 0.55–0.56 mm; SL 0.49–0.50 mm; CI 90–93; SI 87–91; PW 0.42–0.44 mm; PNL 0.21–0.22 mm; PH 0.40–0.41 mm; DPW 0.35 mm; PNI 81–83. Agreeing with holotype in all general features, including details of mandibular, ocular and antennal structure. The eyes range from 0.06 to 0.07 mm in diameter and the scape may exceed the median occipital border by as much as its maximum thickness. Palpal formula: *Maxillary* 2: *Labial* 2 (1 specimen inspected).

The sexual castes, larvae and pupae are not known.

TYPE LOCALITY. NE NEW GUINEA: Aiyura, Eastern Highlands, 1900 m. The type series was taken in a Berlese funnel sample of leafmold from the floor of disturbed rain forest, VI.1962 (R. W. Taylor, acc. 2130). Holotype and paratypes deposited in MCZ collection (Type No. 30922), additional single paratypes in Bishop, BMNH and CSIRO.

RELATIONSHIPS. Apparently allied to the similarly large-eyed members of the *elegantula* group (*borneensis* and *elegantula*). *P. augusta* has a distinctly more primitive habitus than these other species. The broad head, long scapes, coarse sculpturation, distinct mesosomal sutures and raised propodeal angles of *augusta* provide a link between the *elegantula* group and the more primitive, probably archetypical, *P. alpha*. Relationships between the 3 *elegantula* group species are discussed below under *P. elegantula*.

P. augusta occurs in sympatric association with *elegantula* at Aiyura; a single specimen of the latter was included in the Berlese funnel sample which yielded the *augusta* types.

17. *Ponera borneensis* Taylor, new species Figs. 61, 62.

DIAGNOSIS. Known only from the mountains of central Borneo. The basic characters distinguishing this species from its relatives *elegantula* and *augusta* are incorporated in the accompanying key to species of *Ponera*. Details of relationships and diagnostic features of these species are given below under *P. elegantula*.

Worker. HL 0.62–0.65 mm; HW 0.53–0.57 mm; SL 0.46–0.49 mm; CI 86–88; SI 86–89; PW 0.42–0.44 mm; PNL 0.22–0.23 mm; PH 0.41–0.44 mm; DPW 0.36–0.39 mm; PNI 86–90. General form as shown in accompanying figures. Close to *P. augusta* of New Guinea, differing from it in the following characters:

1. Those indicated in the dimensions above—narrower head (*i.e.*, lower cephalic index), relatively high petiolar node, higher petiolar node index.
2. Apical mandibular teeth occupying slightly less than 1/2 the masticatory border, followed by about 10 to 12 minute, indistinct denticles. Palpal formula: *Maxillary* 2: *Labial* 2 (2 specimens dissected).
3. Eyes averaging slightly larger—maximum diameter 0.07–0.09 mm, with about 12 to 16 irregular facets.

4. Scapes shorter, their apices almost exactly reaching median occipital border when they are laid back on head.

5. Mesometanotal and lateral mesonotal sutures much less distinctly marked. The former a more or less distinct incised line, sometimes difficult to see, except in reflected light.

6. Mandibles smooth and shining. Clypeus shining in center, with scattered indistinct punctures; irregularly shagreened at sides. Front of head opaque, coarsely and closely punctate, punctures slightly smaller and more separated than in *augusta*. Sides of head moderately shining, with a cover of medium punctures (diameter *ca* 0.006 mm) separated by distances of slightly more than their maximum diameter. Scapes moderately coarsely shagreened; mesosomal dorsum feebly shining, sculpturation similar to sides of head but slightly more dense; mesonotal puncturation not markedly more dense than pronotum, that of propodeal dorsum less distinctly impressed. Punctures of mesonotum less spaced than those of pronotum and propodeum. Sides of mesosoma strongly shining, almost completely lacking sculpture except for relatively fine longitudinal striation on entire lower halves of mesepisternum and metepisternal areas. Node and gaster moderately shining, with scattered, pilosity-bearing, point punctures. The sculpturation of *borneensis*, particularly that of the sides of the head and the postcephalic areas, is thus considerably less intense than in *augusta*.

8. Pilosity and pubescence as in *P. augusta*.

9. General color dark blackish brown, with reddish brown infuscation on node and gaster, notably on subpetiolar process and gastric apex. Mandibles, antennae and legs bright golden brown.

Worker types. The above description is based on a series of 13 workers. One has been designated as holotype, the remainder as paratypes. The holotype has the following dimensions: HL 0.64 mm; HW 0.56 mm; SL 0.48 mm; CI 87; SI 86; PW 0.42 mm; PNL 0.23 mm; PH 0.43 mm; DPW 0.37 mm; PNI 88.

Paratype ♀♀. 3 alates were originally mounted with the workers described above. One is callow and the others show signs of shrinkage due to drying. This is especially apparent in the node, where the posterior face is fairly strongly concave and the apical crest rather acute in side view. This condition, which is also seen in several paratype workers, is clearly due to contraction of the transverse faces of the node and is not normal for the species. The most intact specimen (MCZ collection) has the following dimensions: HL 0.68 mm; HW 0.58 mm; SL 0.52 mm; CI 85; SI 90; PW 0.53 mm; PNL 0.25 mm; PH 0.49 mm; DPW 0.42 mm; PNI 79; maximum diameter of compound eye 0.21 mm; ocular index 36. Scape almost exactly reaching median occipital border; ocelli distinctly developed; parapsidal lines present. Wing venation of *coarctata* type. Sculpture and coloration as in worker, wing veins very pale yellowish brown. Palpal formula: *Maxillary* 2: *Labial* 2 (callosity inspected).

♂ and larval characters not known. One of the worker paratypes has the remains of a pupal cocoon in its jaws; so *augusta* presumably has enclosed pupae.

TYPE LOCALITY. BORNEO: Mt Tibang, 1500 m (E. Mjöberg), collected from a rotting log.

Holotype and paratypes deposited in MCZ collection; duplicate paratypes, worker and ♀, in BISHOP and CSIRO; workers only in BMNH, Forel Coll., and USNM.

RELATIONSHIPS. See below under *Ponera elegantula*.

18. *Ponera elegantula* Wilson Figs. 35, 63, 64.

Ponera elegantula Wilson, 1957, Bull. Mus. Comp. Zool. **116** (6): 379, worker, ♀. Type locality: Tumnang, Huon Peninsula, NE New Guinea (Holotype and ♀ Paratype examined, MCZ coll.).

DIAGNOSIS. Distinguished from other members of its group by the characters cited below under "relationships." Known only from a few localities at high elevations in NE New Guinea, where it occurs sympatrically with the related *P. augusta* at Aiyura, in the Eastern Highlands.

Additional description. *Worker*: The following notes are based on 19 workers from several accessions made by me at Aiyura, and on the holotype worker (MCZ collection). The Aiyura specimens agree with the holotype in all essential features, but average slightly larger in size. In the general summary of the features of the species given below, special mention is made of the characters of the holotype where they may be significant. Dimensions (holotype cited first): HL 0.70 mm, 0.72–0.74 mm; HW 0.56 mm, 0.58–0.62 mm; SL 0.49 mm, 0.52–0.54 mm; CI 80, 80–83; SI 87, 86–90; PW 0.42 mm, 0.45–0.47 mm (the pronotum of the holotype appears to be pinched through contraction in drying); PNL 0.21 mm, 0.23–0.25 mm; PH (observed but *ca.*) 0.44 mm, 0.46–0.48 mm; DPW 0.38 mm, 0.38–0.41 mm; PNI 88, 83–87 (the relatively high value for the holotype is due to its narrowed pronotum). General features as shown in accompanying figures. The key, figures and dimensions given above should allow easy identification of *elegantula*, the additional specimens permit further qualification of the characters of this species as follows:

1. Posterior 1/2 of masticatory border of mandible with about 6 to 8 minute denticles.
2. Eyes 0.06 mm to 0.08 mm in maximum diameter, with about 11 to 15 facets, situated about 0.92× the distance from lateral occipital border to midpoint of anterior genal border.
3. Scapes failing to reach median occipital border by about 0.2 to 0.5× their thickness.
4. Mesometanotal suture variable in development, completely lacking on mesosomal dorsum in some specimens, including holotype; while other individuals have a very finely incised suture, visible only in strongly reflected light.

Palpal formula: *Maxillary* 2: *Labial* 2 (3 Aiyura specimens dissected).

♀. The dimensions of Wilson's dealate paratype ♀ are: HL 0.76 mm; HW 0.62 mm; SL 0.53 mm; CI 82; SI 86; PW 0.52 mm; PNL 0.25 mm; PH 0.51 mm; DPW 0.44 mm; PNI 85; maximum eye length 0.16 mm; ocular index 26. Similar to ♀ of *P. borneensis* but distinguished by slightly larger size, narrower head, higher scape and petiolar node indices, and relatively small eyes (ocular index 26, opposed to 36 in *borneensis*). Antennal scapes failing to reach median occipital border by about 1/3 their maximum thickness. Sculpturation not markedly reduced relative to *borneensis* ♀, perhaps indicating conservatism in evolution of ♀ structure compared to that of the worker. Propodeal dorsum moderately shining, with scattered medium puncturation (in *borneensis* it is subopaque, coarsely and closely punctate, with a tendency to longitudinal striation in the interpunctural reticulum).

A late pupal ♀ from Aiyura (acc. 2117) agrees with the holotype in general characters, its palpal formula is *Maxillary* 2: *Labial* 2 (dissected).

♂. A single ♂ from Aiyura (acc. 2169) has the following dimensions: HL 0.58 mm; HW (across eyes) 0.65 mm; CI 112; WL 1.15 mm; PNL 0.26 mm; PH 0.40 mm; DPW 0.33 mm; maximum diameter of eye 0.28 mm; ocular index 43. Palpal formula: *Maxillary* 2: *Labial* 2 (dissected), as in ♀ castes. Structure of head, mandibles, antennae, mesosoma, wings, petiole and gaster as in *P. pennsylvanica*. Terminal abdominal sclerites and genitalia conforming to general plan for genus. Pygidial spine stronger than in *P. coarctata*, dorsal process of gonoforceps more strongly developed. Color black, mandibles, legs, antennae and gastric apex very dark brown, wing veins relatively dark brown.

Immature stages: Larvae conforming to general plan for Indo-Australian members of genus, closely resembling those of *P. alpha*, with 3 pairs of dorsal abdominal glutinous tubercles.

DISTRIBUTION AND MATERIAL EXAMINED. NE NEW GUINEA: Aiyura, Eastern Highlands Distr., 1900 m, disturbed rain forest, colony ex "cucujid-stage" rotting log and workers ex Berlese funnel sample, VI.1962 (RWT accs. 2117, 2139); 2000 m, disturbed rain forest, colony ex "zoraptera-stage" rotting log, VI.1962 (RWT acc. 2169). Tumnang, Mongi R. watershed, Huon Peninsula, IV.1955 (EOW acc. 799) (holotype worker and paratype ♀).

RELATIONSHIPS. The 3 members of the *elegantula* group form a fine morphocline in a number of characters. The gradation runs *augusta*→*borneensis*→*elegantula*. *P. augusta* apparently has the most primitive habitus, since it most closely resembles *P. alpha* and *P. selenophora* which are considered to be more primitive than other Melanesian *Ponera*.

The following characters are involved in the morphocline, and presumably indicate tendencies which have taken place in the evolution of *P. elegantula*.

1. Decrease in relative breadth of the head (indicated by cephalic index)—90-93 in *augusta*, 86-88 in *borneensis*, 80-83 in *elegantula*.

2. Decrease in posterior span of antennal scapes, relative to occipital border. They exceed the occiput in *augusta*, almost exactly reach it in *borneensis*, and fail to do so in *elegantula*.

3. Angulation of the posterolateral propodeal edges decreases in intensity. The angles in *augusta* and *borneensis* are about 80°, when viewed from above; in *elegantula* they are slightly less than 90°.

4. Intensity and abundance of sculpturation decreases markedly throughout the series. The gradation from *augusta* to *borneensis* is discussed under the latter species. The sculpturation of *elegantula* differs from that of *borneensis* as follows:

Clypeus shining, apunctate in center, with a few scattered fine punctures at sides. Head feebly shining, covered with punctures about 0.006 mm in diameter, separated by almost the same distance. Sides of head strongly shining, lacking sculpturation apart from pilosity-bearing point punctures. Scapes moderately finely punctate, feebly shining, the punctures separated by intervals about equal to their average diameter. Mesosomal dorsum moderately shining, covered by slightly finer and more widely spaced punctures, than head, closer on mesonotum than elsewhere. Sides of mesosoma almost completely without sculpture, strongly shining. Mesepisterna with a few scattered, moderately large, punctures in holotype, entirely smooth and shining in Aiyura specimens. Longitudinal striation of mesepisternum reduced to a vestigial remnant on its lower posterior edge, that of metepisternal area restricted to the surface over the metapleural gland bulla. Propodeal declivity and

posterior face of node smooth, very strongly shining. Remaining petiolar surfaces shining, without sculpture, apart from minute pilose punctures. Gaster quite strongly shining with small pilosity-bearing punctures separated by distances of about 0.006 mm.

Although the pubescence and pilosity are of similar abundance in *augusta* and *borneensis* there is a marked decline in density of the vestiture in *elegantula*.

19. *Ponera clavicornis* Emery Figs. 33, 65, 66.

Ponera clavicornis Emery, 1900, Természetr. Fü. **23**: 317, pl. 8, figs. 7, 8, worker. Type locality: Friedrich-Wilhelmshafen (=Madang), NE New Guinea. (Syntype examined, Emery coll.).—Mann, 1919, Bull. Mus. Comp. Zool. Harv. **63**: 296, distribution.—Wilson, 1957, Bull. Mus. Comp. Zool. Harv. **116**: 377-379, worker, distribution, ecology; 1958, Bull. Mus. Comp. Zool. Harv. **119**: 327; 1959, Evolution **8** (1): 132, fig. 5, distribution.

DIAGNOSIS. Not easily referable to any of the groups recognized in this study. Known from NE and SE New Guinea, North Queensland, and the Solomon and New Hebrides Islands. Easily recognized by the following combination of characters:

1. Moderately small size (head width 0.43-0.47 mm).

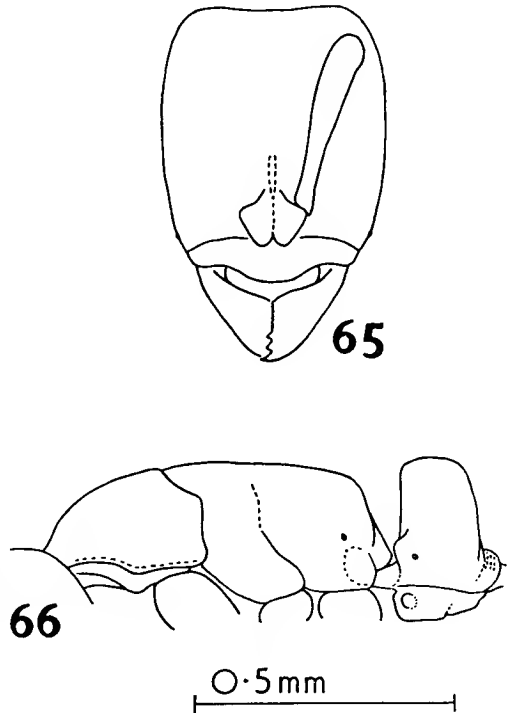
2. Small to medium size eyes, their diameter 0.02-0.05 mm, with 2 to 6 indistinct facets; situated about $0.9\times$ the distance from lateral occipital border to midpoint of anterior genal border.

3. Distinctive heavy sculpturing, especially the regular dense puncturation of head and mesosomal dorsum.

4. Absence of a distinctly incised meso-metanotal suture on mesosomal dorsum (this suture may be represented by a faint impression which does not break the underlying sculpture, but in most specimens it is totally unrepresented).

5. Pilosity very sparse, consisting of a few hairs on mandibles, clypeus, and frontal lobes, the petiolar dorsum, the terminal gastric tergites and all gastric sternites. Erect hairs from cranium and dorsum of mesosoma, and in most samples, from first two gastric tergites.

P. augusta has similar sculpturation but it has a wider head, a distinct mesometanotal suture, and normal pilosity. *P. elegantula* has similarly reduced pilosity and lacks the mes-



Figs. 65-66. *Ponera clavicornis* Emery, worker (Bulolo River Valley, N. E. New Guinea): 65, head; 66, mesosoma and node.

ometanotal suture; it is, however much less heavily sculptured. Both *augusta* and *elegantula* have much larger eyes than *clavicornis*.

Additional description.

Worker: Workers of *clavicornis* should be easily recognized using the keys, figures and diagnostic details presented here. The following qualifications and additions to Wilson's diagnosis should be noted:

1. Known ranges for dimensions and indices (with exception of 1 small individual discussed below) are: HL 0.52-0.59 mm; HW 0.43-0.47 mm; SL 0.35-0.42 mm; CI 81-85; SI 80-89; PW 0.32-0.37 mm; PNL 0.20-0.22 mm; PH 0.28-0.35 mm; DPW 0.27-0.32 mm; PNI 80-89.

2. Palpal formula: *Maxillary 2: Labial 2* (several specimens inspected).

3. Distinct medium clypeal tooth not developed, but a shallow obtuse tumosity may be present in the middle of anterior clypeal border.

4. Scapes failing to reach medium occipital border by a distance of about 1/4 to 1/3 their maximum thickness.

5. The funicular club was said by Wilson to be 5-segmented. Actually the degree of development of the club is quite variable; it may appear to be completely undifferentiated, or rather indistinctly 4- or 5-segmented, even in specimens from a single sample.

6. Lateral mesonotal suture completely absent in most specimens, but a slight, superficial trace of it is present in others. This never completely breaks the sculpturation.

A single worker specimen from Lae, NE New Guinea (T. E. Woodward), has the following dimensions: HL 0.48 mm; HW 0.41 mm; SL 0.32 mm; CI 85; SI 79; PW 0.30 mm; PNL 0.14 mm; PH 0.29 mm; DPW 0.24 mm; PNI 79. This individual agrees with the above *clavicornis* material in general features, but has a relatively low scape index, the scapes failing to reach occipital border by about 1/2 their maximum thickness, and the petiolar node is relatively narrow. It is likely a small nanitic worker of *clavicornis*, in which case the differences in proportions could be due to allometry of a type known to exist in other *Ponera* species. I have determined it provisionally as a member of this species.

♀. Based on 2 alates and a dealate, collected in association with workers at Bisianumu, near Sogeri, SE New Guinea by E. O. Wilson, and 2 dealate ♀♀ from Tumnang and the lower Busu River, NE New Guinea (E. O. Wilson). The last specimen was not associated with workers, but seems to be satisfactorily placed under *clavicornis*.

The Bisianumu ♀♀ have the following dimensions and indices: HL 0.55-0.57 mm; HW 0.47-0.49 mm; SL 0.38-0.40 mm; CI 85-86; SI 81-83; PW 0.44-0.46 mm; PNL 0.17-0.18 mm; PH 0.36-0.39 mm; DPW 0.31-0.33 mm; PNI 70-72; maximum diameter of compound eye 0.15-0.16 mm; ocular index 31-34; palpal formula: *Maxillary 2: Labial 2* (1 specimen inspected). Differing from workers in usual characters of full sexuality, resembling them in color, development of sculpturation, pubescence and pilosity. Wing venation of "*coarctata* type."

DISTRIBUTION AND MATERIAL EXAMINED. All known records of *P. clavicornis* are listed below. I have seen material from all these series, except that reported by Mann (1919). SE NEW GUINEA: Bisianumu (Wilson 1957). NE NEW GUINEA: Madang, Bubia, lower Busu River, Tumnang (Wilson 1957); Bulolo River valley, 6 km NE of Wau, 1100 m, ex

Berlese funnel sample, leafmold, rain forest, VI.1962 (RWT) MCZ; Lae, ex leafmold, rain forest, 6.VIII.1956 (T. E. Woodward) CSIRO; Stephansort, Astrolabe Bay (Biro) Emery coll.,—syntype worker. SOLOMON IS.: *Guadalcanal*: Kukum, 10.I.1963 (P. Greenslade) MCZ; Mt. Austen, 11.II.1963 (P. Greenslade) MCZ. *Santa Isabel*: (Mann 1919). NEW HEBRIDES: *Espiritu Santo* and *Malekula* (Wilson 1957). AUSTRALIA: *Queensland*: Northern Cape York Peninsula (P. J. Darlington) MCZ.

Identified material of *P. clavicornis* has been deposited in the following collections: BRISBANE, BMNH, CSIRO, USNM.

GEOGRAPHIC VARIATION. Wilson (1957) found that workers from Bisianumu had relatively abundant pubescence on the dorsa of the first 2 gastric segments. Those from Tumnang and the New Hebrides had these segments bare of pubescence, while the geographically intermediate Bubia specimens were intermediately pilose. The new material from Lae, Guadalcanal and Cape York all lacks this pilosity. Wilson also reported geographic variation in scape index between New Guinea (SI 86-89) and the New Hebrides (SI 80-84). My 2 Guadalcanal specimens have SI 85-88; and the 2 Cape York ones have SI 81-83.

ECOLOGY. I encountered *clavicornis* in midmontane oak, *Araucaria klinkii* rain forest near Wau, NE New Guinea. Wilson found it to be ecologically very adaptable and collected it in primary and secondary lowland forest, foothill forest, and true midmountain forest under a variety of conditions. Altitudinal range of the collections is from sea level to 1500 m in New Guinea, as well as from high elevation forest on Guadalcanal. The only reported nest series was taken under bark on a "passalid-stage" rotting log (Wilson 1957). It is interesting that this geographically widespread species should show wide ecological amplitude.

RELATIONSHIPS. *P. clavicornis* is apparently not close to any other known *Ponera* species. Its heavy sculpturation is unusual and probably represents a secondary adaptation, since most of the other features of this ant mark it as a fairly derived form. These characters include its small size, short scapes, the tendency towards differentiation of a funicular club, the very reduced pilosity and lack of a dorsal mesometanotal suture. Apart from its peculiar sculpturation and pilosity *clavicornis* is somewhat similar to the members of the *japonica*, *leae* and *tenuis* species groups discussed below and may represent a somewhat divergent product of the stock linking these forms back to the larger, more primitive *Ponera* species, such as those of the *oreas* and *taipigensis* groups.

Ponera japonica Group

A group of 3 species: *japonica* Wheeler (Japan, Malaya and Java), *incerta* (Wheeler) (Java, E. Melanesia, Samoa) and *swezeyi* (Wheeler) (Samoa and Hawaii). The diagnostic characters are: (1) antennal funiculus with an indistinctly to distinctly differentiated 5-segmented club; (2) mesometanotal suture of worker incised on mesosomal dorsum. These species are brown to yellowish brown in color and of small to medium size (head width 0.29-0.50 mm). They form a probably morphocline sequence: *japonica*→*incerta*→*swezeyi*. Characters involved in this morphocline include reduction in size, in number of eye facets, in distinctness of the median clypeal denticle, in length of the scapes, in relative breadth of the petiolar node, and in the intensity of coloration.

The larvae are known for *incerta* and *japonica* (Teranishi 1940) and are typical for Indo-

Australian *Ponera*. Pupal cocoons occur in *incerta* and *swezeyi*, but no pupae of *japonica* are available. The males of *incerta* have the primitive palpal formula: *Maxillary* 4: *Labial* 2.

These species are all widespread, and evidently have considerable capacities for active dispersal, and for distribution by man, especially in Eastern Melanesia and Polynesia. They are probably derived, through *japonica*-like stock, from ancestors at about the *sinensis/taipingensis* grade of organization.

20. *Ponera japonica* Wheeler Figs. 67-69.

Ponera japonica Wheeler, 1906, Bull. Amer. Mus. Nat. Hist. **22**: 306, worker, ♀. Type locality: Yamanaka, Suruga (West slope, Hakone Mts), Japan (Syntypes examined—MCZ, AMNH); 1928, Boll. Lab. Zool. Portici **29**: 99, distribution.—Emery, 1909, Deutsche Ent. Zschr. 307, fig. 8.—Santschi, 1937, Bull. Soc. Ent. Belg. **77**: 364, distribution; 1941, Mitt. schw. ent. Ges. **18**: (4/5): 273, distribution.

Ponera (Hypoponera) japonica: Santschi, 1935, Ann. Soc. Ent. France **43**: 79.

Ponera japonica var. *crocea* Santschi, 1941, Mitt. schw. ent. Ges. **18** (4/5): 273, worker. Type locality: Namase, Honshu (Syntypes examined—Santschi coll.). *Nec. Ponera crocea* Roger, 1860. **New Synonymy.**

This species was erroneously identified as *Ponera scabra* by Hayashida (1957, 1960) in his fine studies on the ecology of Hokkaido ants; specimens from various Hokkaido localities loaned by Dr Hayashida for this study are clearly referable to *P. japonica*. Dr Hayashida has checked additional specimens in his collection and finds that none are referable to *P. scabra* (*in litt.*).

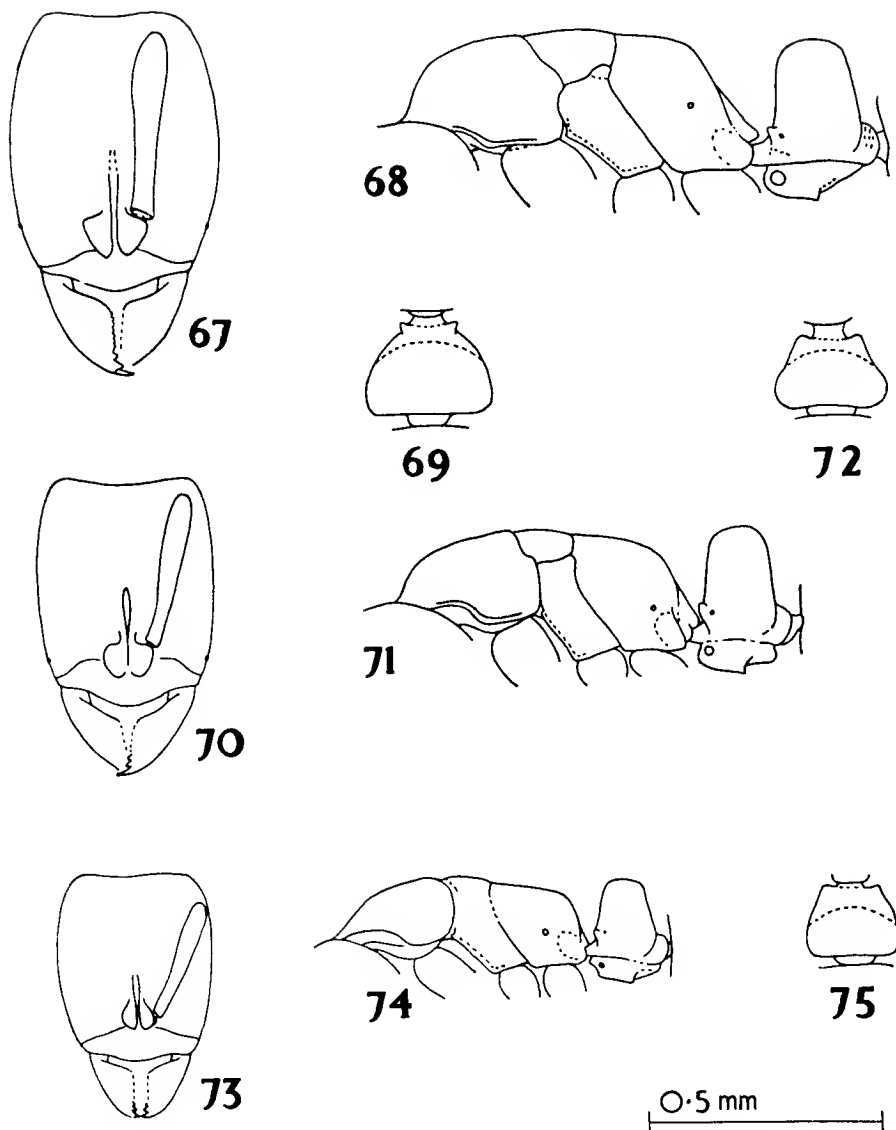
Three syntype workers of *Ponera japonica* st. *formosae* Forel (1913, Archiv Naturg. (A) **79** (6): 186) described from Anping, Taiwan, prove to be referable to the widespread tramp species *Hypoconerops gleadowi* Forel (**New Synonymy**).

The synonymy of variety *crocea* is based on examination of 3 syntype workers from the Santschi collection; they have been directly compared with the *japonica* types (MCZ collection).

TYPES. Wheeler, as usual, designated no holotype from his original series of *P. japonica*. A worker (MCZ collection) with the measurements given below is here designated *lectotype* and is so labeled. Four additional syntype workers in the MCZ collection and 8 in the AMNH, along with 2♀♀ (one in each of these collections) have been designated and labeled as *paralectotypes*.

DIAGNOSIS. *P. japonica* is an exceptionally widespread and rather variable species, known currently from Japan, Malaya and Java. It is probably widespread on the SE Asian mainland, and could also occur in western Indonesia, Melanesia, Taiwan and the Philippines. The workers may be recognized by the following characters:

1. Dimensions: HL 0.53-0.63 mm; HW 0.42-0.50 mm; SL 0.36-0.43 mm; CI 77-83; SI 80-91; PW 0.32-0.38 mm; PNL 0.17-0.21 mm; PH 0.34-0.40 mm; DPW 0.25-0.30 mm; PNI 74-91.
2. Antennal funiculus with a distinctly to indistinctly 5-segmented club.
3. Mesometanotal suture clearly incised on mesosomal dorsum.



Figs. 67-75. Group of *Ponera japonica*. *Ponera japonica* Wheeler, worker (Syntype): 67, head; 68, mesosoma and node; 69, node, dorsal view. *Ponera incerta* (Wheeler), worker (Poentjak, Java): 70, head; 71, mesosoma and node; 72, node, dorsal view. *Ponera swezeyi* Wheeler (Syntype): 73, head; 74, mesosoma and node; 75, node, dorsal view.

The antennal club, while indubitably 5-segmented in all specimens I have seen, is sometimes rather indistinctly so. The expression of mesometanotal sutural character may also be weak, but no difficulty should be encountered in using this character.

P. japonica is larger than the other members of its group, the head widths of which

never exceed 0.40 mm. It may be differentiated from its Japanese congener, *P. scabra*, by its much smaller size (head width 0.61-0.64 mm in *scabra* workers), 5-segmented club, and less intense sculpturation.

MATERIAL EXAMINED AND DISTRIBUTION. I have examined specimens used in establishing most previously published records of *japonica*, except those of Santschi (1941) and Teranishi (1940). The Santschi records are probably dependable, as other specimens from his collection are correctly identified. The Teranishi Korean record is suspect and could not be checked since the Teranishi collection was lost during World War II (*teste* K. Yasumatsu, *in litt*). JAPAN: Asahigawa, 31.VII.1960 (K. Hayashida); Hakodate, 9.VIII.1960 (Hayashida); Sapporo area (Hayashida 1957; 1960—recorded in error as *Ponera scabra*); Shadai, 29.IX.1960 (Hayashida). Honshu: Iwakuni, Yamagushu (Santschi, 1941); Mt Ibuki, Shigaken (Santschi 1941); Namase, 16.VIII.1921 (C. Teranishi) Santschi coll. (*crocea* syn-types); Nikko (Wheeler 1928); Yamanaka, W. slope Hakone Mts (*Type locality*)(H. Sauter) MCZ, USNM. KOREA: Shakuoji (Teranishi 1940). MALAYA: The Gap, Frazer's Hill, near Kuala Lumpur (A. M. Lea & wife) CSIRO. INDONESIA: Java: Poentjak (?Poentjakgaroe), 5.VII.1929, MCZ; Tjibodas, 1400-1500 m, 8.VII.1920-VIII.1921, MCZ.

Additional description and geographical variation.

Worker: Most of the required additional description involves the geographically variable characters discussed below.

The various series studied have the following dimensions (given in mm/100) and indices.

	Type series Number 13	" <i>crocea</i> " types 3	Hokkaido series 9	Javanese series 7	Malayan series 3
HL	56-60	60-61	60-63	53-58	53-54
HW	45-47	47-48	49-50	43-47	42-43
SL	37-40	40	39-43	37-41	36-37
CI	78-82	77-80	79-82	80-83	79-81
SI	80-85	83-85	80-86	84-91	84-88
PW	34-37	36-37	36-38	32-36	33
PNL	18-20	21	20-21	17-18	17
PH	34-37	37-38	37-40	34-37	35
DPW	25-28	28-29	28-29	26-30	28-30
PNI	74-80	78	76-78	81-85	85-91

Other variable characters include the following: (1) The posterior span of the scapes relative to the median occipital border. They fail to reach the occiput by a distance of $1/2$ - $1/3$ their maximum thickness in the Honshu and Malayan specimens, while in the Hokkaido and Javanese samples their apices are about contiguous with the median occipital border. (2) The median clypeal tooth is weak, and barely raised in anterior view in the Honshu and Javanese material. Its minimal development is about the same in the Hokkaido and Malayan specimens, in the former however, it ranges up to a distinct low tumosity and in the latter it attains maximum development as a distinct tooth, nearly as wide as high. (3) The mesometanotal suture is strongly to moderately developed in Ja-

panese and Javanese examples. In Malayan specimens, however, the suture is more weakly incised; maximally it is only as strong as that of the weakest Japanese specimen.

Variation is also shown in the degree of development of a lobate salient at the posterodorsal corner of the mesepisternum (fig. 68). This presumably represents an atavistic remnant of the metanotum, or mesepimeron. In Japanese material it is distinct and separated from the episternum by a suture-like impression. It is similarly developed in the Javanese specimens, but the "suture" is absent. The Malayan specimens have a less protrusive lobe lacking a suture.

In all of the material certain features show little variation: palpal formula: *Maxillary 2: Labial 2* (specimens from each sample dissected); eyes small with 1 to 5 indistinct facets. Antennal club distinctly to indistinctly developed. Lateral mesonotal suture always present, with variation in intensity of its incision paralleling that of the mesometanotal suture. Dorsum of the node, viewed from above, about equal to, or slightly less than, a half-circle in extent.

No consistent character or set of characters allows logical separation of the material into more than one species. The only discontinuous feature is the value for petiolar node index, which ranges 74-80 in Japan, 81-85 in Java and 85-91 in Malaya. These values for the 3 major series run in the reverse order to their rank based on mean head width, so that the observed data might be due to negative allometry of petiolar node width, relative to head width. Evidence concerning the true status of these forms will be forthcoming only when further material is available. The Malayan and Javanese specimens have been placed in the CSIRO and MCZ collections, prominently labeled as "voucher specimens", with a reference to this work.

♀. Two Japanese syntypes have the following dimensions: HL 0.65 mm; HW 0.53 mm; SL 0.45 mm; CI 81; SI 85; PW 0.46 mm; PNL 0.22 mm; PH 0.43 mm; DPW 0.33-0.34 mm; PNI 72-74; maximum diameter of compound eye 0.15 mm; ocular index 28; palpal formula: *Maxillary 2: Labial 2* (1 inspected).

Males and immature stages are not available for study. Teranishi (1940) figured a larva supposed to be that of *japonica*. He showed 3 pairs of dorsal abdominal glutinous tubercles, as in all other Oriental-Australian species.

ECOLOGY. Detailed information is given by Hayashida (1957, 1960), concerning the ecology of *japonica* (erroneously identified as *P. scabra*). It is not uncommon, though sparsely distributed, in the vicinity of Sapporo, on the Ishikari Plain of Hokkaido, an area once extensively forested but now largely urban or cultivated. Of 28 ant species collected there it was 18th in abundance (18 or 1.3% of 1491 colonies taken in a total of 43 hours collecting, divided equally between 8 habitat types). *P. japonica* apparently has fairly broad habitat preferences and was taken in the following situations: (1) arid sparsely vegetated sand dunes or river sides (50% of the 18 colonies); (2) dry sparsely vegetated, disturbed cropfields or roadsides (6% of colonies); (3) rather humid pastures and meadows with dense grass and herb cover and loamy clay soil (22% of colonies); (4) humid woods or forests with low insolation, loamy soils and abundant decaying matter lying on the ground (22% of colonies). It was not taken at the sea shore, in peat bogs, or on the margins of wood lots. The general parameters of habitat preference were given as low light intensity, and moderate moisture conditions (Hayashida 1957). Foraging is restricted to the ground layer, as usual in *Ponera*.

In woods and grasslands nests were in or under humus and other debris, but in more open habitats *japonica* was found nesting among the roots of grasses or in exposed soil, even where it was sandy. If debris or stones were available in open habitats nests were usually constructed beneath them. In the arid sand dunes or dry river beds about 75% of colonies were under stones.

The slight apparent preference by *japonica* for open dry areas, opposed to forested ones, may be biased due to the greater probability of locating a colony in an open area than a forested one, in a given standard unit of time. Nevertheless it is clear that the species has wide ecological tolerance; a factor which has probably been of significance in its distributional history. I have noted in field studies in New Zealand, Fiji and Panama that typically forest dwelling cryptobiotic ants may often be taken under stones in cleared areas adjacent to forests, although such nesting sites are usually not preferred within the forest, where most nests are found in or under rotting wood fragments, branches or logs (see also Wilson, 1959).

RELATIONSHIPS. *P. japonica* is apparently widespread in the Orient and Indonesia. Its relationships at the species group level clearly lie with *incerta* and *swezeyi*, the distributional ranges of which are peripheral to the SE Asian mainland. These latter species are in fact almost certainly derived from *japonica*-like stock. The supposed phylogenetic relationships within the *japonica* group thus agrees well with prevailing zoogeographic theory concerning origins of the Melanesian and Polynesian faunas.

The relatively large size, the tendency to develop a median clypeal denticle, the large eyes, the relatively long scapes, and the broad petiolar node, mark *japonica* as the most primitive species of its group. These features also imply ancestral relationship of *japonica* to stock of about the *sinensis-taiipingensis* group grade of organization.

21. *Ponera incerta* (Wheeler) Figs. 70-72.

Pseudocryptopone incerta Wheeler, 1933, Amer. Mus. Novitates, **692**: 18, fig. 7, worker, ♀.

Type locality: Depok, Java (Holotype examined—MCZ coll.).

Ponera incerta: Wilson, 1957, Bull. Mus. Comp. Zool. **116** (6): 384, notes on holotype.

Ponera ratardorum Wilson, 1957 Bull. Mus. Comp. Zool. **116** (6): 369, worker, distribution, variation, ecology. Type locality: St. Paul's, Baining Mts, New Britain (holotype and paratypes examined, MCZ coll.); 1958, *Ibid.* **119** (4): 337; 1958, *Evolution* **13** (1): 125, fig. 5, zoogeography. **New Synonymy.**

SYNONYMY. Study of the extensive material of this species now available has allowed synonymy of *ratardorum* under *incerta*. At the time of Wilson's 1957 monograph only the unique headless *incerta* holotype was known from Java. Its postcephalic structure, and Wheeler's description of cephalic characters, appeared to differentiate it from a closely related Melanesian species which was described by Wilson as *P. ratardorum*. Subsequently an additional undamaged Javanese worker, clearly conspecific with the *incerta* holotype, has been found (MCZ collection); several Solomon Is. specimens have come to hand, and several hundred individuals of all castes are available from the Samoan Islands.

In the light of this material the characters of Wilson's key (1957: 359, couplet 5) break down completely, and other characters will not allow differentiation of more than one

species. It is now clear that the color variation in Wilson's specimens was due to fading of the older material. The structure of the antennal club and variation in the dorsal profile of the posterior petiolar border no longer provide useable taxonomic characters; since the range of variation shown by these structures in the non-Samoan material is duplicated among specimens from those islands. Some variation is present between the available samples, but it is not considered taxonomically significant (see below).

DIAGNOSIS. Easily recognized by moderately small size (head width 0.36-0.40 mm in the worker, 0.43-0.44 mm in the ♀), additional to the characters of the *japonica* group (distinctly to indistinctly 5-segmented antennal club, and clearly incised dorsal mesometanotal suture in the workers). In the *japonica* group head width range is diagnostic—*japonica* is larger than *incerta* (worker (HW 0.42-0.50 mm) and *swezeyi* is smaller (worker HW 0.29-0.33 mm). *P. incerta* is sympatric with *japonica* on Java, and with *swezeyi* on Samoa; in other parts of its range the species group characters are diagnostic.

♀. Easily assigned to the *japonica* group on the basis of the 5-segmented antennal club, relatively small size and brown coloration. Within the group size also allows identification of ♀♀, and there are wing venational differences.

P. incerta is superficially similar to the sympatric *P. tenuis* on Samoa; the latter species is distinguished by its 4-segmented club, lack of a mesometanotal suture in the worker, and the absence of pupal cocoons in all castes.

Additional description and variation.

Worker: Dimensions and indices for all available workers are shown in Table 1.

The values for 20 randomly selected Samoan specimens, no more than 1 from a single collection, almost match the entire known ranges for the species. In fact, the overall variation in dimensions can be matched completely in this material.

Other characters include:

1. Scapes failing to attain median occipital border by about 2/3 to 1/4 their maximum thickness in Indonesian and E. Melanesian material. Most Samoan specimens have slightly longer scapes, which may almost reach the occipital border.

2. Apical 5 funicular segments forming a club, which varies in distinctiveness but is always easily discernable.

3. Mesometanotal suture (contrary to Wheeler's description) finely and distinctly incised on mesosomal dorsum of holotype and the additional Javanese specimen. The sutural impression is here less intense than in the Melanesian examples, where it is usually very distinct. The range of variation is covered in the Samoan material; so this character cannot be accorded taxonomic significance.

4. Posterior face of the petiolar node, viewed from above, shows all intermediate conditions from shallowly concave to weakly convex. The additional Javanese specimen differs from the holotype in this character; where the latter has a feebly concave face, that of the former is very weakly but distinctly convex. A similar range is shown by the Samoan material.

5. Palpal formula: *Maxillary 2; Labial 2* (6 Samoan specimens dissected).

♀. Known only from Samoa. The following notes are based on 6 alate and dealate specimens, no more than 1 from a single sample, collected on all 3 major islands. HL

Table 1. *Ponera incerta* (Wheeler)—Ranges for standard dimensions (mm/100) and indices shown by workers from various localities

	JAVA		NEW BRITAIN AND NEW HEBRIDES	CAROLINE IS.	SOLOMON IS.	SAMOA	TOTAL RANGES
	<i>incerta</i> holotype	Tamarang specimen	<i>ratardorum</i> type series				
Number	1	1	4*	1**	2	20	29
HL	—	49	46-48	49	44-46	45-50	44-50
HW	—	39	36-38	38	37-38	36-40	36-40
SL	—	34	30-32	33	31-32	30-34	30-34
CI	—	80	78-80	78	83-84	78-83	78-84
SI	—	87	83-86	87	84	84-87	83-87
PW	29	31	27-30	29	27-29	28-30	27-30
PNL	15	15	14-15	—	15	13-15	13-15
PH	31	31	28-31	—	28-29	28-32	28-32
DPW	22	23	19-22	—	21-22	19-23	19-23
PNI	76	74	68-78	—	76-78	68-79	68-79

*HL, HW, SL, CI, SI and PW after Wilson (1957), remaining measurements by me.

**Measurements after Wilson (1957); I have not seen this specimen.

0.51-0.53 mm; HW 0.43-0.44 mm; SL 0.36-0.38 mm; CI 83-84; SI 84-86; PW 0.36-0.37 mm; petiolar node length 0.15-0.16 mm; petiole height 0.34-0.35 mm; dorsal petiole width 0.26-0.28 mm; PNI 72-76; maximum diameter of compound eye 0.14-0.15 mm; ocular index 32-34; palpal formula: *Maxillary* 2: *Labial* 2 (2 specimens dissected). Differing from the workers in the usual characters and complying with basic plan of structure for the genus. Wing venation of "*coarctata* type."

♂. Known only from 3 specimens collected by Ettershank (his accessions 69 and 71) and associated with workers in Berlesates from Tiapapata, Upolu. Dimensions: HL 0.42-0.44 mm; HW (across eyes) 0.41-0.44 mm; CI 97-100; Weber's length of mesosoma 0.71-0.77 mm; petiolar node length 0.14-0.16 mm; petiole height 0.23-0.26 mm; dorsal petiole with 0.16-0.19 mm; maximum diameter of compound eye 0.20-0.21 mm; ocular index 48-49; palpal formula: *Maxillary* 4: *Labial* 2 (1 specimen dissected, others inspected). General features, and details of terminal abdominal sclerites and genitalia typical for *Ponera*. Wing venation as in ♀.

IMMATURE STAGES. Larvae with 3 pairs of glutinous abdominal tubercles. Pupae of all castes enclosed in cocoons.

DISTRIBUTION AND MATERIAL EXAMINED. A particularly widespread species. I have examined all material listed below, except that from the Caroline Is. *Incerta* will almost certainly be found eventually in E. Indonesia, New Guinea, and possibly Fiji. INDONESIA: *Java*: Depok, 7. VIII. 1923 (Dammerman) MCZ, holotype worker; Samarang (Jacobson) MCZ. CAROLINE IS.: *Yap*: (R. J. Goss) (Wilson 1957). NEW BRITAIN: St. Paul's, Baining Mts., Gazelle Peninsula, 350 m, 5.IX.1955 (J. L. Gressitt) MCZ, type of *P. ratardorum*.

NEW HEBRIDES: *Espiritu Santo*: Ratard Plantation, near Luganville, 7-13.I.1955 (E. O. Wilson) MCZ. SOLOMON IS.: *Guadalcanal*: Mt. Austen, 4.II.1963 (P. Greenslade) MCZ. *Santa Cruz*: Grasciosa Bay, 1916 (W. M. Mann) USNM. SAMOA: (Collectors G. Ettershank, R. W. Taylor and T. E. Woodward given by initials.) *Savaii*: Gagaifomauga, berlesates ex ground and moss on logs, rain forest, 14.VI.1962 (GE accs. S2, S4-6); Letui, ground berlesate, rain forest, 22.III.1962 (RWT acc. 597); Lotogo, 350 m, near Vaisala, stray from leafmold in crotch of *Ficus* tree, 30 m above ground level, rain forest, 21.III.1962 (RWT acc. 459); Mt Matafa, 700 m, berlesates ex ground and moss on trees, rain forest, 24.III.1962 (RWT accs. 588, 590); Mt Matafa Road, 200 m, nest under bark on log, rain forest edge, 19.III.1962 (RWT acc. 370); Mt Olomanu, tree moss berlesates, rain forest, 14.VI.1962 (GE accs. S7, S11); Samalae'ulu, ground berlesate, coastal rain forest, 22.III.1962 (RWT acc. 596). *Upolu*: Unless otherwise stated all records are from "ground layer" berlesates of soil, leafmold, leaf litter or moss. Afiamalu, 700 m, beating foliage, 11.VI.1940 (E. C. Zimmerman); strays and colonies under moss and bark on logs, disturbed rain forest, 9-17.III.1962 (RWT accs. 222, 247, 254, 313, 342, 350); berlesates, moss ex ground and rotten logs, disturbed rain forest, 6.I.1956 (TEW); III-IV.1962 (RWT accs. 256, 283, 301, 302, 584, 2315-2317, 2319-2324; GE accs. 24, 46, 47, 50-54); tree moss berlesates, disturbed rain forest, III-IV.1962, less than 2 m above ground (RWT accs. 232, 262, 300, 335), 10 m above ground (RWT accs. 580, 2307, 2308, 2312), 8 m above ground (GE acc. 44), 15 m above ground (GE acc. 37); Aleisa, rain forest, 4.IV.1962 (GE accs. 25, 29, 30, 32); Fagaloa, rain forest, 13.V.1962 (GE acc. 68); Falealili District, rain forest, 29.III.1962 (RWT acc. 637); above Falevao, 200 m, rain forest, I.1956 (TEW); Lauli'i, 5.I.1956 (TEW); Le Mafa, rain forest, 16.I.1956 (TEW); dealate queens, ex roadside clay bank, berlesate, rain forest, 29.III.1962 (RWT acc. 634, 638); 13.V.1962 (GE accs. 65, 66); Malololelei, 650 m, rain forest, 19.I.1956 (TEW); Poutasi, 2.II.1956 (TEW); Salea Puga, coastal Futu forest, 10.I.1956 (TEW); Tanumalala, rain forest, 2.II.1956 (TEW); Tiapapata, berlesates, moss ex logs and trees, rain forest, 19.V.1962 (GE accs. 69-72, 74-76); Togitogiga, 400 m, rain forest, 12.V.1962 (GE accs. 56, 60); Utumapu, 130 m (TEW). *Tutuila*: All records below are based on Berlese funnel samples collected in rain forest by G. Ettershank on 13.VII.1962, unless otherwise specified. Accession numbers refer to Ettershank material, MCZ collection. Alega, leafmold, coastal Futu grove, 26.I.1956 (TEW); Alo'au, 450 m, moss ex logs (accs. T16-T20); Le Mafa, 250 m, ground moss, and moss ex newly felled tree (accs. T2, T8, T10); Malaeimi, leafmold, coastal rain forest (accs. T21-T24); Ridge between Mts Oloava and Olomanu, 460 m, epiphytes, and moss ex logs (accs. T11-T15); Tafuna, leafmold and soil, rain forest, 24.I.1956 (TEW).

ECOLOGY. No data is available from Indonesia. New Britain specimens are from a rain forest berlesate, and the New Hebrides specimens were foraging diurnally in leaf litter in primary coastal rain forest (Wilson 1957). In my experience *incerta* is common in rain forest on all 3 main Samoan Islands, and was present at all elevations which were worked. At Afiamalu, it was extremely common in an area of disturbed rain forest where it had apparently undergone local irruption. This area consisted of about 20 acres of previously rich forest which had been partially cleared to allow access to cattle. About two-thirds of the canopy trees and most of the lower story elements had been felled, apparently some 18 to 20 months previously. Much of the smaller timber had decayed or been removed, but the larger logs remained, generally in sound condition, and rotting branch fragments of up to 10 cm diameter were abundant on the ground. This forest was very wet, moss

being plentiful on the ground and especially on the upper surfaces of the fallen logs, where thick cushions were developed. The standing trees were festooned with mosses and epiphytes which appeared more abundant than in the adjacent undisturbed forest.

Ants were plentiful in this area and included a number of probably introduced forms such as *Ponera incerta*, *P. tenuis*, *Cryptopone testacea* (Emery), *Odontomachus simillimus* Fr. Smith, *Strumigenys rogeri* Emery, *Pheidole umbonata* Mayr, *Pheidole sexspinosus* Mayr, *Solenopsis papuana* Emery, and *Nylanderia vaga* (Forel). Some of these had penetrated the adjacent rain forest but were much less abundant than in the cleared area. Apparently endemic species included *Ponera loi*, *Ponera woodwardi*, *Ectomomyrmex insulanus* Mayr, and one undescribed species each in *Vollenhovia*, *Rogeria* and *Pheidole*. All of these were markedly more abundant than in the less disturbed rain forest. Most of the species listed above were nesting in rotting wood fragments, in decayed patches on the undersides of logs, or under the moss attached to their upper surfaces. Most species were taken in Berlese funnel samples of moss gathered from the standing trees at heights of up to 16 meters above ground.

In addition to *P. incerta* the similar *P. tenuis* is present on Samoa. In most localities, especially lowland ones, no evidence of ecological differences between these species was observed. Both were common in Berlese funnel samples of leafmold or moss, from the ground layer, or from trees, with no indication of habitat divergence between them. This was the case at localities such as Le Mafa, Tanumalala, and Tiapapata on Upolu, or Gagaifomauga and the Mt Olomanu-Mt Matafa area on Savaii. At Afiamalu, however, the habitat was apparently partitioned between the two such that *incerta* was dominant in moss from the ground or on logs (i.e., "ground layer"), whereas *tenuis* was found almost exclusively in tree moss.

The following table summarizes the distribution of the two species in 49 Berlese funnel samples of either tree or ground layer moss from Afiamalu.

	Number of Samples	Samples with <i>incerta</i>	Samples with <i>tenuis</i>	Both Present	Neither Present
Tree Moss	24	9	8	2	9
Ground Layer Moss	25	20	2	2	5

Observe that *incerta* is significantly less abundant in tree moss than on the ground ($X^2_1 = 7.48$, the probability that the values represent chance deviation from a random distribution being much less than 0.01). *P. tenuis*, on the other hand, is more abundant in tree moss samples ($X^2_1 = 3.40$, p less than 0.10). When the 4 parameters of columns 2 and 3 of the table are considered in a single test the statistical probability that the 2 species are randomly distributed is less than 0.03 ($X^2_3 = 5.40$).

If the ecological displacement hypothesis is applied in this case we must conclude that *incerta* is dominant on the ground, to the almost complete exclusion of *tenuis*; while the latter species is more successful in the tree moss niche. The displacement of *tenuis* from the ground layer may be even more pronounced than indicated by the above data. The 2 ground moss records of *tenuis* represent single workers, and this species was never collected by hand from the ground layer, while *incerta* was continually encountered there. Conversely the ground moss samples usually contained good series of *incerta*, often includ-

ing portions of nesting colonies with brood; while 3 of the 9 *incerta* tree moss records were single dealate, probably claustral, queens, which may not have been destined to survive to produce colonies in any case.

RELATIONSHIPS. See above under *P. japonica*.

22. *Ponera swezeyi* (Wheeler) Figs. 8, 73-75.

Pseudocryptopone swezeyi Wheeler, 1933, Amer. Mus. Novitates **672**: 16-17, fig. 6, worker, queen. Type locality: vicinity of Honolulu, Hawaii.

Ponera swezeyi: Wilson, 1957, Bull. Mus. Comp. Zool. **116**: 370.

DIAGNOSIS. Known only from the Hawaiian and Samoan Islands. Easily recognized by the combination of small size (worker head width 0.29-0.33 mm, ♀ HW 0.32-0.33 mm) with the characters of the *japonica* group (5-segmented antennal club, and incised mesometanotal suture). In addition, the ♀ wing venation (and presumably that of ♂) is peculiar. The 2nd abscissa of Rs+M arises distal to the anterior base of the medio-cubital crossvein (m-cu) (fig. 8). This character occurs in only one other *Ponera* species, the much larger *P. chapmani* (Philippine Islands).

P. swezeyi is the only known *Ponera* occurring in Hawaii. In Samoa it is easily distinguished from its congeners by its smaller size and light coloration.

Only 3 other species (*petila*, *szaboi* and *szentivanyi*) are known to have HW values less than 0.34 mm; they all have 4-segmented antennal clubs, and lack the dorsal mesometanotal suture.

Additional description

Worker: Wilson's (1957) measurements and indices require modification because of additional material: HW 0.29-0.33 mm; HL 0.38-0.44 mm; SL 0.25-0.28 mm; CI 72-78 mm; SI 84-85; PW 0.21-0.24 mm; PH 0.24-0.26 mm; DPW 0.18-0.19 mm. There is no apparently significant structural variation between the Hawaiian and Samoan material.

Wheeler (1933) stated that eyes were not present in *swezeyi* workers; an opinion accepted by Wilson (1957). Examination of Samoan specimens and re-examination of the types, indicates that eyes *are developed* in this species. They consist of minute single facets, lying about 0.84-0.86× the distance from the lateral occipital border to the midpoint of the anterior genal border. They are distinctly pigmented in fresh specimens, but fade on drying. Palpal formula: *Maxillary* 2: *Labial* 2: (2 Upolu specimens dissected). Mesometanotal suture finely but distinctly incised on mesosomal dorsum.

♀. [Notes based on 2 Hawaiian specimens (including a syntype), and 4 Samoan ones, 3 from Upolu, 1 from Tutuila]: HL 0.42-0.43 mm; HW 0.32-0.33 mm; SL 0.26-0.28 mm; CI 76-78; SI 81-85; PW 0.27-0.28 mm; PNL 0.13-0.14 mm; PH 0.25-0.28 mm; DPW 0.19-0.20 mm; PNI 71-74; maximum diameter of compound eye 0.09 mm; ocular index 27-28; palpal formula: *Maxillary* 2: *Labial* 2 (1 Samoan specimen dissected). Agreeing with the generic plan for this caste, and differing from workers in the usual characters. Wing venation peculiar and diagnostic, as described above under "diagnosis."

♂ unknown.

Immature stages: Larvae are not available for study; worker pupae, and presumably those of the other castes, enclosed in cocoons.

DISTRIBUTION AND MATERIAL EXAMINED. Until now *P. swezeyi* has been recorded only from Hawaii, and was considered by Wilson (1957) to have probably been introduced there by man. This opinion has been supported by discovery of the species on Samoa, where it is widespread on all 3 main islands. In the list below G. Ettershank, R. W. Taylor and T. E. Woodward are referred to by their initials. Unless otherwise stated all material is from the MCZ collection. **SAMOA:** *Savaii*: Mt Matafa, 700 m, ground berlesate, rain forest, 15.III.1962 (RWT acc. 590). *Upolu*: Afiamalu, 700 m, berlesates, moss ex rotten logs, disturbed rain forest, 9, IV. 1962 (GE accs. 46, 48); tree moss berlesate, 8 m above ground, disturbed rain forest, 9.IV.1962 (GE acc. 45); above Falevao, 200 m, ground berlesate, rain forest, I.1956 (TEW); Lauli'i, 17.I.1956 (TEW); Le Mafa, workers and alate queen, nests in clay bank, 29.III.1962 (RWT acc. 634); berlesate, moss ex clay bank, 30.III.1962 (RWT); 2 dealate queens, ground berlesate, rain forest, 13.V.1962 (GE acc. 65); Togitogiga, 400 m, berlesate, debris ex rotten log, rain forest, 12.V.1962 (GE acc. 59); Vaipoto, ground berlesate, rain forest, 9.I.1956 (TEW). *Tutuila*: winged queen at light, 3.VI.1958 (W. Keller); Tafuna, Berlese funnel sample, soil and leafmold, rain forest, 26.I.1956 (TEW). **HAWAII:** *Oahu*: vicinity of Honolulu (TYPE LOCALITY), 3 syntype workers and a ♀; Herring Valley, workers and dealate queen, 30.VII.1933 (F. X. Williams); Kamoo, in soil under pineapple plants, 22. VII. 1935 (W. Carter) USNM; Mt Olympus Trail, 600 m (recorded by Williams (1937)—not seen by me).

ECOLOGY. The only Samoan nest records are those from Le Mafa, Upolu. Several colonies were found at this site, about 1.5 meters above ground level, in an almost vertical clay road cutting, in an area of rather disturbed rain forest. *P. swezeyi* appears to differ in nesting preferences from the other small Samoan species (*incerta* and *tenuis*), colonies of which were almost always taken in rotting logs, or under moss on logs or trees. Occasional *swezeyi* workers were taken in moss berlesates but no nests were found in such sites, and the only sexuals taken were from soil/leafmold samples. This apparent preference for soil nesting may have been important in the distributional history of *swezeyi*, which would thus readily be carried by Polynesian and European man in soil attached to root crops such as taro or kumara, sugar cane or pineapple plants, etc. Recall that most Hawaiian records are from soil in pineapple plantations.

One wonders whether *swezeyi* is a Samoan autochthon secondarily introduced into Hawaii, or whether it has reached these island groups from a third source area, presumably in E. Melanesia. The new records from primary rain forest at high elevations on Upolu and Savaii could indicate that it is a Samoan autochthon. However, the Samoan fauna contains numerous introduced species, including some not usually considered tramps, though clearly carried to the islands by man. Most of the latter are, like *P. swezeyi*, cryptobiotic or soil-nesting forms, which could easily have been transported in soil attached to plant roots.

RELATIONSHIPS. Close to *P. incerta*, with which it may be cognate.

23. *Ponera manni* Taylor, new species Figs. 76, 77.

DIAGNOSIS. A highly aberrant species, known only from Viti Levu, Fiji Is. Distinguished by the following set of characters. Size moderately large (head width 0.57 mm); eyes single-faceted, placed well back on the relatively strongly convex sides of the head; petiolar node narrow (petiolar node index 73); antennal funiculus lacking a distinctly differentiated club;

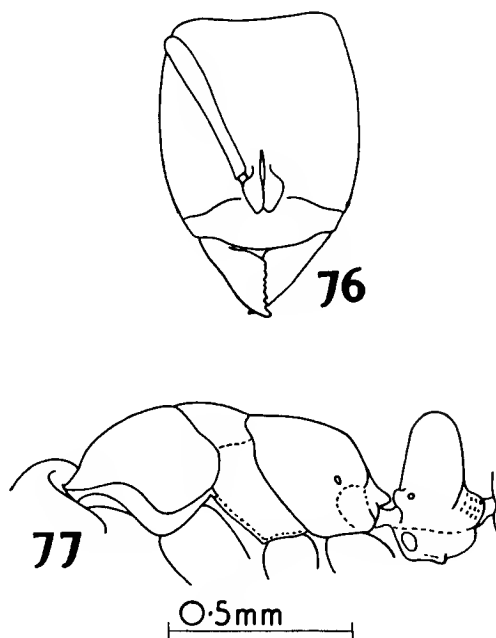
mesometanotal suture clearly incised on mesosomal dorsum. This is the only known *Ponera* species with HW exceeding 0.43 mm, which has a PNI less than 77.

P. manni is easily separated from the only other Fijian *Ponera* of similar size (*P. colaensis*) by the combination of larger size (HW 0.50–0.54 mm in *colaensis*); relatively broad head (cephalic index 89; 81–83 in *colaensis*); distinctly incised mesometanotal suture; narrower petiolar node (PNI 86–91 in *colaensis*); and lighter color.

Holotype worker. HL 0.64 mm; HW 0.57 mm; SL 0.47 mm; CI 89; SI 82; PW 0.41 mm; PNL 0.21 mm; PH 0.41 mm; DPW 0.30 mm; PNI 73. Mandibles triangular; outer borders slightly sinuate; masticatory border with 3 strong teeth occupying the apical 2/5 of its length, followed by a series of 7 distinct obtuse denticles, which appear in the worn mandibles of the type to have been subequal in size, and about 1/2 as large as the smallest of the apical teeth. Head as in fig. 76; occipital border moderately concave; sides relatively strongly convex. Leading edge of clypeus almost straight; anterior face with a raised obtuse median

longitudinal tumosity. Palpal formula: *Maxillary* 2: *Labial* 2 (inspected). Eyes minute, single-faceted, about 0.01 mm in diameter, situated about $0.8\times$ the distance from lateral occipital border to median anterior genal border. Scapes noticeably more slender than usual in *Ponera*, almost exactly reaching median occipital border when laid back on head. Funiculus also relatively slender, distinctly expanded apically, but no definite segmental club differentiated; apical segment about equal in length to the 2 preceding together. Mesosomal profile as in fig. 77. Mesometanotal suture very distinctly marked; lateral mesonotal suture reduced to a faint vestige. Propodeal sides and declivity almost straight, when viewed from above; posterolateral edges forming angles of about 90° in dorsal view. Form of node as in fig. 77. Subpetiolar fenestra distinct, oval; posterolateral teeth acute.

Mandibles smooth and highly polished. Clypeus moderately shining, indistinctly shagreened. Head subopaque, finely and closely shagreened. Scapes moderately shining, very finely punctate. Dorsum of mesosoma fairly strongly shining, with very shallow, somewhat effaced, puncturation. The punctures less than 0.01 mm in diameter, spaced at intervals about equal to their average diameter on pronotum; somewhat closer on mesonotum; those on propodeal dorsum less distinct and more sparsely scattered. Sides of mesosoma more strongly shining than dorsum, with similar but more scattered punctures. The usual longitudinal striation of the metepisternal area represented by weak vestiges of such sculpturation.



Figs. 76–77. *Ponera manni* n. sp., worker (Holotype): 76, head; 77, mesosoma and node.

Petiolar node shining, finely punctate. First 2 gastric tergites feebly shining, with a close cover of moderately large, irregular, pilosity-bearing punctures.

Short fine erect to sub-erect pilosity moderately abundant on mandibles, clypeus, frontal lobes and dorsum of pronotum; sparse on remainder of head and mesosoma. Similar, slightly longer, pilosity moderately abundant on petiolar dorsum and entire gaster, where hairs on ventum and apex are longest. Fine pubescence fairly abundant on head and antennae, gaster and legs; rather sparse on mesosoma and petiole, except pronotal dorsum and apex of node.

Color dull medium reddish brown, legs and gastric apex slightly paler.

TYPE LOCALITY. FIJI IS.: *Viti Levu*: Mt Lomolaki, near Nandarivatu, 17.II.1962 (R. W. Taylor, acc. 22).

The unique holotype was taken under a stone in wet soil on the floor of slightly disturbed rain forest at about 1000 m elevation. This most unusual species is named for the late Dr W. M. Mann, a pioneering myrmecologist in Eastern Melanesia.

TYPE DEPOSITION. Holotype in MCZ collection (Type No. 30924).

RELATIONSHIPS. The general features of *manni* are so peculiar and anomalous that easy placement in any of the Indo-Australian species groups of *Ponera* is impossible. The size, long scapes and lack of a differentiated antennal club might seem to relate it to the *sinensis-taipingensis* series of species groups. However, I think these characters are convergent, and that *manni* is in fact an extremely enlarged descendant of stock close to *P. japonica*. The single faceted eyes, placed relatively far back on the head, the low petiolar node index, the form of the propodeum and node, the sculpturation and the coloration all support this notion.

The long scapes and simple non-clubbed funiculi may have been produced by "counter-current" tendencies correlated with size increase in evolution from a *japonica*-like ancestor. Short antennal scapes, and a segmentally differentiated funicular club are correlated with small size in *Ponera*, in smaller *Hypoponera* species of the *abeillei* group, and in small *Cryptopone* species. The fact that the clypeus of *manni* is very narrow, relative to the head capsule, may be correlated with secondary increase in size of the cranium in the descent of this species.

Ponera leae Group

The group includes two rather small light brown species (head width 0.36-0.44 mm), *P. leae* Forel of E. Australia, New Caledonia, Norfolk I., and northern New Zealand, and *P. exotica* M. R. Smith, originally described from the SE United States, but almost certainly of Indo-Australian origin. These species superficially resemble the smaller members of the *japonica* and *tenuis* groups. They have distinctly 4-segmented antennal clubs, like the *tenuis* group species, but differ from them in possessing a distinctly incised mesometanotal suture in the worker caste. Females are known for both species, they are typical for the genus. All specimens are dealated; so the wing venation is unknown. Males and larvae are not available. The single pupa studied, that of a *leae* worker, was enclosed in a cocoon,

24. *Ponera leae* Forel Figs. 78-80.

Ponera leae Forel, 1913, Bull. Soc. Vaud. Sci. Nat. 49: 175, worker. Type locality: Tasmania

(Holotype examined, Forel coll.).—Taylor, 1960, *Pacific Science* **14**(2): 178, fig. 1, redescription, distribution.

Ponera leae subsp. *oculata* Wheeler, 1927, *Proc. Amer. Acad. Arts Sci.* **62**: 130, fig. 1, worker, queen. Type locality: Norfolk I. (Syntypes examined, MCZ) (nec. *Ponera oculata* Fr. Smith, 1858).

Ponera leae subsp. *norfolkensis* Wheeler, 1935, *Occ. Pap. Bishop Mus.* **11**(11): 13 (*nom pro* *P. oculata* Wheeler, 1927). **New Synonymy.**

Ponera norfolkensis: Taylor, 1960, *Pacific Science* **14**(2): 179.

Ponera caledonica Wilson, 1957, *Bull. Mus. Comp. Zool.* **116**(6): 361, worker, ♀, distribution. Type locality: Ciu, near Mt Canala, New Caledonia (Holotype and Paratypes examined, MCZ).—Taylor, 1960, *Pacific Science* **14**(2): 180. **New Synonymy.**

Ponera exceedra Wilson, 1957, *Bull. Mus. Comp. Zool.* **116**(6): 364, worker, ♀. Type locality: Arthurs Seat, Victoria, Australia, (Holotype and Paratypes examined, MCZ). **New Synonymy.**

SYNONYMY. My present concept of this species is considerably changed from those of Wilson (1957) and Taylor (1960). Where 4 species (*leae*, *exceedra*, *caledonica* and *norfolkensis*) have been recognized, it is now clear that only one exists. In 1960 I followed Wilson's concepts of *exceedra* and *caledonica* and surveyed characters apparently distinguishing the former from *leae*, and enabling recognition of *norfolkensis* as a separate species. Little material was then available, indeed, *leae* was virtually unknown from the Australian mainland. The species is now known extensively in the Brisbane and Sydney areas, due to the efforts of Woodward and Lowery. Material from N. Queensland was taken in 1962 by me, and a few valuable Tasmanian examples have been located in the CSIRO collection. About 80 Australian and Tasmanian specimens are thus in hand, where only 4, the *leae* and *exceedra* types, were previously available. In addition material from Paihia, New Zealand (Taylor 1960) has been increased considerably by specimens collected by me in 1959.

Key characters "distinguishing" these erstwhile species included differences in size, development of the eyes and scapes, in shape of the petiolar node, viewed from above, and in color and sculpturation. These characters are all variable in Australian material, and can no longer be accorded taxonomic significance. No other characters appear to allow retention of any of the names published subsequently to Forel's *leae*. I will not discuss each new synonymy in turn; since their justification is fully accommodated in the discussion below.

DIAGNOSIS. Easily recognized by moderately small size, and presence of the *leae* group characters (distinctly 4-segmented antennal club and clearly incised mesometanotal suture in worker). Differentiation of *leae* and *exotica* is discussed below under the latter species.

Only 2 other *Ponera* species are known to occur in Australia, namely *clavicornis* and *selenophora*. Both are widespread Melanesian elements which have been taken in Australia only at the extreme northern tip of Cape York. They are much larger than *leae* and easily distinguished from it.

DISTRIBUTION AND MATERIAL EXAMINED (fig. 78). The following material of this species has been studied; it includes every specimen which I know to exist. The collectors, B. B. Lowery, R. W. Taylor, E. O. Wilson and T. E. Woodward, are listed by initials. The Woodward material is deposited at the University of Queensland; the Lowery specimens

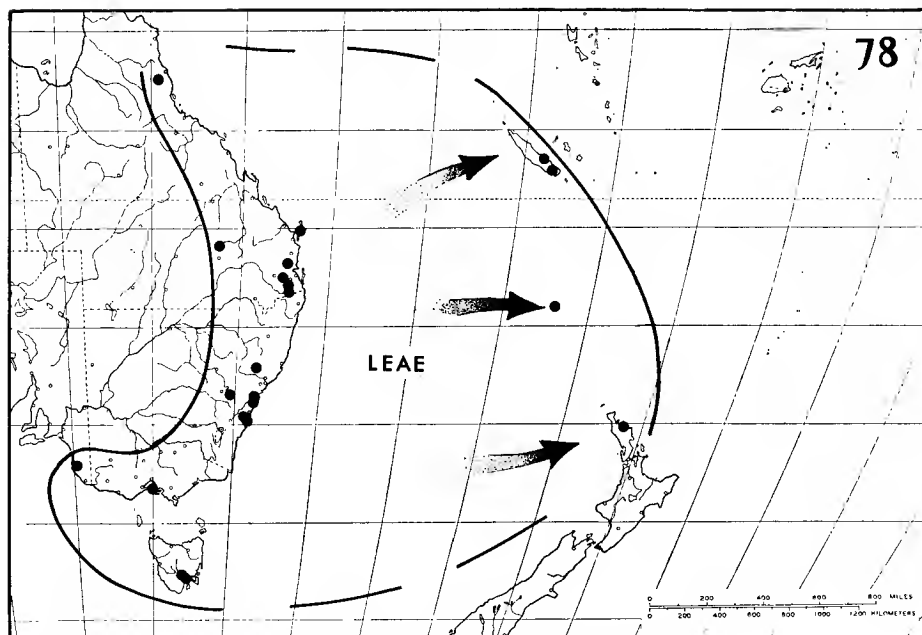


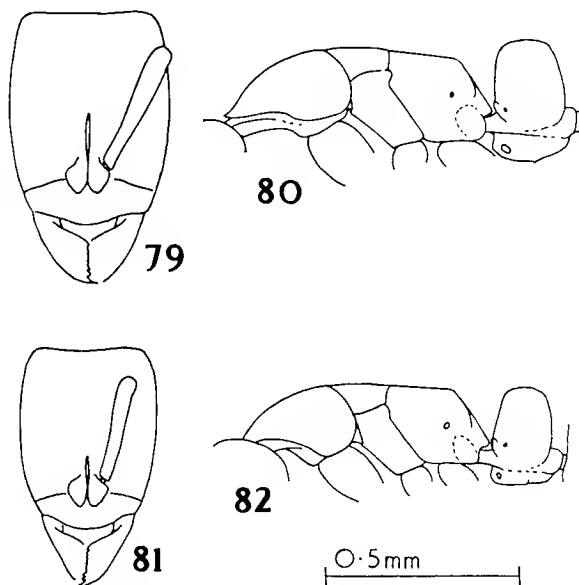
Fig. 78. *Ponera leae* Forel. Distribution.

are from his collection or CSIRO; unless otherwise specified other material is in the MCZ collection. **AUSTRALIA:** *NE Queensland:* Atherton Tableland, 16 km from Atherton on Herberton Road, 790 m, rain forest, leafmold berlesate, 3 workers, 22.VI.1962 (RWT acc. 1694); ex rotting wood fragment, forest floor, 1 dealate ♀, 1.VI.1962 (RWT acc. 1569). *SE Queensland:* Carnarvon Gorge, leaf litter berlesate, 5 workers, 26.III.1954 (TEW). Woody Island (=Frazer Island), Middle Hill Flat, leafmold berlesate, 1 worker, 12.IX.1953 (E. J. Reye) Queensland U. coll. Mapleton, ex rotting log, disturbed rain forest, 1 worker, 1 ♀, 27.V.1962 (RWT acc. 1276). Mt D'Aguilar Range, 600 m, ex rotting log, rain forest, 3 workers, 4.V.1962 (RWT acc. 817). Tamborine Mountain, east side below Eagle Heights, rain forest leafmold berlesate, 3 workers, 8.V.1953 (TEW); N. side near Curtis Falls, rain forest leafmold berlesate, 3 workers, 8.V.1953 (TEW). Binna Burra, rain forest leafmold berlesate, 8 workers, 1 ♀, 7.IX.1952 (TEW). Mt Clunie east spur, rain forest leafmold berlesate, 2 workers, 5.IV.1959 (Lamington National Park, rain forest leafmold berlesate, 10 workers, 1.VI.1955 (TEW). *New South Wales:* Barrington Tops, rain forest leafmold berlesate, 3 workers, 22.XII.1954 (TEW). Wentworth Falls, 600 m, under rock sandstone plateau, 1 worker, 3.V.1960 (BBL). *Sydney:* Cowan, deep sandstone valley, rain forest fringe, 1 worker, 1.III.1959 (BBL); Pymble, dry forest, 1 dealate ♀, 23.X.1960 (W. L. Brown) MCZ; Middle Harbour, under rock, deep sandstone valley, 1 dealate ♀, 6.IX.1956 (BBL); Riverview College, Lane Cove River, damp shady foreshore, 1 worker, 28.IV.1959 (BBL); National Park, Bola Creek, under stone, rain forest, 5 workers, 26.VII.1959 (BBL); 6 km E of Berry, heavy *Eucalyptus* forest, 1 worker, 16.XII.1960 (BBL); 6 km NW of Berry, 450 m, under stone, rain forest, 5 workers, 1 dealate ♀, 18.XII.1960 (BBL); Gerroa, Crooked River, ex rotting log, sea level rain forest, 5 workers, 19.XII.1960 (BBL). *Victoria:*

Arthurs Seat, McCrae, 120-270 m, under rock, open *Eucalyptus-Banksia* woodland, 28.IV.1951 (W. L. Brown) (holotype of *P. exceedra*) MCZ coll. South Australia: Lucindale, 1 dealate ♀ (A. M. Lea) MCZ coll. *Tasmania*: (Type locality) No further data (A. M. Lea) (holotype of *P. leae*) Forel coll.; Hobart, 6 workers (A. M. Lea) CSIRO coll.; Mt Wellington, 1 worker (A. M. Lea) CSIRO coll. NEW ZEALAND: *North Auckland*: Paihia, Bay of Islands, 1.I.1958, 3 workers (K. P. Lamb) Plant Diseases Division, D.S.I.R., New Zealand, coll.; Berlese funnel sample, forest leafmold, 9 workers, 7.II.1959 (RWT), Auckland Museum, CSIRO, MCZ. *NORFOLK I.*: No further data, 2 syntype workers of *norfolkensis*, MCZ coll.; and a dealate ♀, CSIRO (all A. M. Lea). The latter has labels identical to the syntypes and was possibly collected with them. *NEW CALEDONIA*: I have seen Wilson's complete *caledonica* type series consisting of 18 workers and a dealate ♀. The localities are: Ciu, near Mt Canala; Mont Mou; Chapeau Gendarme. Ecological details are given by Wilson (1957).

This widespread ant, like other small *Ponera* species (*exotica*, *incerta*, *swezeyi* and *tenuis*), probably owes its great range in part to dispersal by man. This conclusion may seem surprising, considering the rarity of *leae*, its cryptobiotic habits, and lack of indications that it is in any way associated with man. It has, however, become obvious in recent years that the dispersal of such relatively insignificant ants by human agency is very common. Consider such wide ranging and discontinuously distributed cryptobiotic species as the ponerines *Syscia typhla* (Roger), known under various names from China, Nepal, Okinawa, Hawaii, Samoa and Puerto Rico (Wilson & Taylor mss); *Hypoponera eduardi* (Forel) known from Europe and New Zealand (Brown 1958); and *H. opaciceps* (Mayr) recorded from North and South America, the Antilles, the Philippines, New Caledonia and parts of Polynesia (Wilson & Taylor mss). Notable also are the dacetines *Trichoscapa membranifera* Emery (SE United States, E. China, Fiji Is., Samoa, Hawaii, and the West Indies (Wilson & Taylor mss), *Strumigenys rogeri* Emery (essentially pantropical, Brown, 1954) and *Quadri-*
struma emmae Emery (widely scattered in the tropics and subtropics, Brown 1949).

Other ecologically similar Australian ants have ranges similar to *P. leae*. *Amblyopone australis* Erichson is even more widespread, extending into SW Australia, New Guinea, Lord Howe I. and the New Hebrides as well as all areas where *leae* occurs. Also notable are *Orectognathus antennatus* Fr. Smith (S. Queensland, New South Wales, Victoria and



Figs. 79-82. Group of *Ponera leae*. *Ponera leae* Forel, worker (Tasmania): 79, head; 80, mesosoma and node. *Ponera exotica* M. R. Smith, worker (N. Carolina): 81, head; 82, mesosoma and node.

northern New Zealand), and *Strumigenys perplexa* (SW and SE Australia, Tasmania, Norfolk I., Lord Howe I. and North I., New Zealand). It seems likely that the New Zealand, Norfolk I., and Lord Howe I. populations of these species represent human introductions (Brown 1958; Taylor & Wilson 1961).

The single known New Zealand population of *P. leae* is interesting since it is apparently restricted to the Paihia area. This now small township in the Bay of Islands district was one of the first European settlements in New Zealand and was an important and populous port of call for much shipping during the early parts of last century. Although many ships would have arrived under full cargo, it is likely that some, especially whalers and timber carrying vessels, would have arrived under ballast. (This would almost certainly be true of ships seeking Kauri timber (*Agathis australis*) which was coveted by Australian shipbuilders for masts and spars.) Although the evidence is circumstantial it seems likely that *leae* may have been carried to New Zealand in soil ballast by such vessels. This opinion is suggested by Lindroth's study of trans-North Atlantic faunal dispersal (1957), especially his chapters dealing with the ballast transport of Carabidae from SW England to Newfoundland. *P. leae* is not the only Australian ant introduced into New Zealand, and apparently restricted to the Bay of Islands. The E. Australian *Pheidole yarrensii* Forel is abundant there, and is apparently more widespread, having been recorded about 100 km further north at Whangaroa, and at Kaikohe, 32 km inland from Paihia (Cumber 1959). The distribution of *P. yarrensii* might represent a further stage in expansion from a point-of-introduction at the Bay of Islands.

It seems probable that *leae* is a relatively recent human introduction into New Zealand, and this is also likely for the Norfolk I. population. In New Caledonia, on the other hand, *leae* could well be a native species. Species level relationships between the New Caledonian and Australian faunas are fairly common (Wilson 1959), probably indicating extensive pre-human movement of propagules from Australia to its island neighbor.

Additional description and variation. The worker and ♀ castes were adequately described in recent papers of Wilson (1957) and Taylor (1960). These did not mention the presence of an incised mesometanotal suture on the worker mesosomal dorsum or that the palpal formula in both ♀ castes is *Maxillary 2; Labial 2* (verified here by dissection). The ♂♂, the ♀ wing venation and larval characters are not known; a worker pupa from Mapleton, Queensland is enclosed in a cocoon.

In Australia *leae* is quite variable, but the whole range of variation is encompassed by series from limited areas, and variability seems to be largely ecotypical rather than geographical.

The dimensions of various worker series are shown in Table 2. No trends in geographical variation are indicated by these measurements, apart from a tendency for the New Caledonian specimens to have relatively low scape index values. Considerable range is shown for most dimensions even in single samples; especially in the larger ones.

In order to analyse this size variation, and other characters, I have studied in detail the workers collected near Sydney (including all New South Wales material listed above except that from Barrington Tops). These specimens show ranges for the standard quantitative characters which are almost co-extensive with those of the total Australian sample, yet all were collected within a radius of about 80 km. Though there is variation from sample to sample in mean size (*i.e.*, head width), this is completely intergradient when all specimens

Table 2. *Ponera leae* Forcl. Ranges for standard dimensions and indices shown by workers from various localities.

Localities*	1	2	3	4	5	6	7	8	9	10	Range of samples 1-10	
Number of specimens	3	5	1	17	3	18	1	7	2	12	69	18
HL	48-55	51-53	55	51-56	51	49-55	53	53-55	54	50-55	48-56	51-52
HW	37-41	39-40	41	39-44	39	37-42	38	40-41	42	38-40	37-44	38-40
SL	32-36	33-34	36	34-39	34	31-36	34	35	36	32-33	31-39	32-33
CI	75-77	75-78	75	76-78	77	73-78	72	73-76	78	73-76	72-78	73-77
SI	86-88	85-87	88	85-90	90	84-89	89	85-87	86	85-87	84-90	80-86
PW	28-32	29-31	33	30-34	30	27-32	30	30-31	33	28-30	27-34	27-30
PNL	18-20	19-20	20	18-20	19	17-20	20	18-21	18-20	18-21	17-21	17-18
PH	30-32	29-31	32	31-35	29-30	27-33	30	29-32	33-35	28-30	27-35	29-31
DPW	23-26	23-26	26	24-29	23	21-26	24	24-25	26-27	22-25	21-29	22-25
PNi	81-83	83-84	79	80-85	79	76-85	80	80-83	79-82	79-83	76-85	76-83
LPI	59-63	65-67	64	57-62	63-66	57-64	67	63-67	59-60	63-64	57-67	57-62

* Localities

1. Atherton Tableland, Qld.
2. Carnarvon Gorge, Qld.
3. Frazer Island, Qld.
4. Brisbane Area, Qld.
5. Barrington Tops, N. S. W.
6. Sydney Area, N. S. W.
7. Victoria (*excedra* holotype)
8. Tasmania (incl. *leae* holotype)
9. Norfolk I. (*oculata* types)
10. Paihia, New Zealand
11. New Caledonia

are considered (see Table 3 below). Other variable characters include color, sculpturation and pubescence, relative breadth of the head and relative width and height of the petiolar node. Variability in these features is correlated with the size of the specimens, *i.e.*, the expression of each character follows an allometric progression.

Two phase logarithmic plots of the standard dimensions, HL, PW, SL, PNW and PH, plotted against HW show the following allometric relationships:

1. Head length negatively allometric relative to head width ($k \approx 1.3$), hence larger specimens tend to have relatively short heads, yielding *higher* CI values.

2. Pronotal width and scape length approximately isometric relative to head width.

3. Petiolar node width and petiole height positively allometric relative to head width ($k \approx 0.7$, and $k \approx 0.8$ respectively). Larger specimens thus tend to have relatively high and wide petiolar nodes than do smaller ones. Since head width and pronotal width are approximately isometric the PNI values of large specimens tend to be higher than those of small ones.

There is also allometric variation in thickness of the petiolar node, viewed from the side. Petiolar node length is negatively allometric relative to petiole height ($k \approx 1.2$), so the node appears less bulky in larger specimens than in small ones. When viewed from above its area is relatively greater in smaller specimens, and its dorsum varies in shape from distinctly more to slightly less than a half-circle.

Color variation ranges from bright yellowish brown in smaller specimens, to dull light medium brown in larger ones. Sculpturation of larger specimens is distinctly more intense than in smaller ones. The cephalic punctures of small specimens are separated by shining interpunctural areas, and spaced at distances slightly greater than their maximum diameter, while those of the large specimens are tightly packed, and the head is opaque. Pilosity of the larger specimens is slightly more abundant, and distinctly longer and thicker than in smaller ones. All these characters intergrade in intermediate-sized specimens.

The frequency distribution of specimens of various size classes in samples from the Sydney area is shown in Table 3.

Note that the specimens in the first 4 columns (Riverview—Wentworth Falls) are smaller than those of the last column (National Park), while the Berry specimens are of intermediate size. If these tendencies are considered with available ecological details we may suggest that the variation is correlated with ecological factors. The samples are, of course, limited and the small specimens of the left hand column could be nanitics; in which case the apparent tendencies would be random attributes of the material. The Riverview and Cowan samples are from sandstone country with light, porous soils, relatively low in humus. The Riverview specimen is from rather sparse *Eucalyptus* forest on the foreshore, and the Cowan specimen from a deep sandstone gully, at the fringe of a rain forest patch. The Gerroa specimens were taken in a small disturbed patch of rain forest at sea level.

The large National Park specimens are from rain forest; more dense, more heavily shaded, and with more moist, darker soil than the preceding sites. The Berry material includes a single specimen (the largest) from heavy *Eucalyptus* forest, and the remainder are from rain forest at 450 m elevation.

It appears that mean size of workers may be influenced by ecological factors, possibly soil moisture, texture, and insolation. Although color, sculpturation and pilosity apparently

Table 3. *P. leae* Forel: Size distribution of workers [various New South Wales samples.]

Dimensions (mm/100)		Sample					
HL	HW	Riverview	Cowan	Gerroa	Wentworth Falls	Berry	National Park
49	37	1					
50	37		1	1	1		
50	38			3		1	
51	38					1	
51	39			1			
52	38					1	
52	39					1	
52	40					1	
53	41						1
54	42					1	1
55	42						2

vary allometrically in the Berry series, there is relative discontinuity between them and the Riverview-Gerroa material on one hand, and the National Park specimens on the other. Thus, if the specimens truly illustrate general phenomena for this species, individuals of *leae* from sparse *Eucalyptus* forest on dry sandstone soils would be expected to have paler color and less intense sculpturation and pilosity than *identically sized* specimens from rain forest, just as they would be paler in color, less densely sculptured and less hirsute than larger specimens from their own populations. Variation shown by series from other localities may be explained on similar grounds.

P. leae emerges as a single species, with relatively little geographical variation *per se*, but with considerable variation in local material throughout its range. The erstwhile species *excedra*, *norfolkensis* and *caledonica* are easily accommodated within this range of variation. Material from southern Australia is limited; that available shows higher frequency of lightly colored and sculptured individuals than in the north. *P. leae* may penetrate drier habitats, where pale colored variants are produced, more successfully in the south than in the north. The northern rain forests are sharply differentiated from relatively dry sclerophyll woodland from which *P. leae* is apparently absent, and from which it may be excluded by excessive dryness. It is thus fairly precisely restricted to true rain forest, or to relic rain forest patches. In the south, however, the wetter sclerophyll forests are not sharply defined from drier types, but grade fairly gently into them. Consequently *leae* may have relatively dry situations, near the lower threshold of its habitat preference, more readily available here than in the north. The species may thus be generally more lightly colored and sculptured in the south than in the north.

This situation is comparable with that in *P. coarctata*, which also produces pale colored, relatively weakly sculptured forms, in drier habitats. Such variants are more common in the drier Mediterranean, Black Sea and Caspian areas than in more northern localities in Britain, France, Germany or E. Europe. Detailed study of variation in these two species would be of considerable interest. In the case of *leae* it might shed light on factors re-

sponsible for the high variability of a number of E. Australian ants, notably *Amblyopone australis* Erichson (Brown 1960) and *Mayriella abstinens* Forel (Wheeler 1935; Taylor 1961).

RELATIONSHIPS. See below under *P. exotica*.

25. *Ponera exotica* M. R. Smith Figs. 81, 82.

Ponera exotica M. R. Smith, 1962, Acta Hymenopterologica 1 (4): 378, worker, ♀. Type locality; Croatan National Forest, North Carolina, United States (Holotype and Paratype examined—USNM).

DIAGNOSIS. A species originally described from North Carolina, and recorded here from Oklahoma. The affinities of *P. exotica* seem to be with the Indo-Australian fauna, rather than with the N. American endemic *P. pennsylvanica*. It has probably been introduced into the United States from the Indo-Australian area, where it has not yet been collected.

Exotica is similar to *P. leae*, from which it is distinguished by the characters of couplet 26 of the key presented above. This couplet unequivocally separates all specimens studied here; its complexity reflects the close similarity between these species. *Exotica* is easily distinguished from the sympatric *pennsylvanica* by its much smaller size, 4-segmented antennal club; lack of a mesometanotal suture, and much paler coloration.

DISTRIBUTION AND MATERIAL EXAMINED. I have examined numerous North Carolinian specimens, including the whole type series, and much additional material furnished by Dr W. G. Carter. About 100 specimens from Oklahoma were also provided by Carter. *North Carolina*: Beaufort Co.: W. of Acre; Craven Co.: Croatan National Forest, 3 km W. of Croatan (*Type locality*); NW of Havelock; S. of New Bern. Duplin Co.: between Faison and Calypso. New Hanover Co.: E. of Wilmington. Orange Co.: W. of Hillsboro. Union Co.: near Indian Trail (vicinity of Charlotte). *Oklahoma*: McCurtain Co.: one series. Payne Co.: four series.

These records are all from Berlese funnel samples of leaf litter or leaf mold. All except one (Beaufort Co., N. C., D. L. Wray) were gathered by Carter. The Beaufort Co. collection represents the first record of this species; it is dated September 1950. Carter's North Carolina records were made in June through early September 1960; the Oklahoma ones in July and August, 1963.

Additional description and variation in workers. Little data additional to the original description is necessary, apart from the discussion of worker variation. The palpal formula of both ♀ castes is *Maxillary 2: Labial 2* (3 Oklahoma workers and a ♀ dissected). Immature stages, ♂♂, and the ♀ wing venation are not known.

The various series from the 2 major localities, North Carolina and Oklahoma, have the dimensions given in Table 4.

No apparently significant dimensional differences are present between these samples. Non-quantitative variation is as follows: North Carolina specimens duller in color than Oklahoma ones, which are bright golden brown, opposed to dull medium brown. Impression of mesometanotal suture, strong in both series, but more distinct in Oklahoma material. Oklahoma specimens very slightly less densely sculptured than those from North Carolina. This small amount of variation is not surprising, considering that shown by *P. leae*.

ECOLOGY. Conditions at each North Carolina collection site were reviewed in detail by

Table 4. *Ponera exotica* M. R. Smith: Dimensions of workers from major collection areas. The North Carolina sample includes the entire type series. Measurements in mm/100.

Locality	No.	HL	HW	SL	CI	SI	PW	PNL	PH	DPW	PNI	LPI
North Carolina	24	46-50	36-40	28-32	77-83	75-82	26-29	15-17	26-30	20-23	72-81	50-59
Oklahoma	20	48-52	38-41	31-34	77-80	81-85	28-31	15-16	26-30	19-23	70-76	52-57

M. R. Smith (1962). I quote here from Carter's (1962b) summary of the ecology of this species in North Carolina.

"Specimens were collected in a xeric piedmont post oak—blackjack forest near Hillsboro and in a dry, sunny post oak—blackjack oak stand southeast of Charlotte. The coastal plain collections were obtained from well-shaded mesic forests of loblolly pine—hardwood—beech, loblolly pine, pine—dogwood, pine—hardwood, and oak—loblolly pine."

It may be significant that higher elevation records on the piedmont plateau were from more xeric, less heavily shaded stations, with thinner leafmold and litter than the lower lying coastal plain sites. It would be interesting if an elevational shift in ecological preferences could be demonstrated.

Carter gives the following descriptions of the Oklahoma stations (pers. comm.). "Payne County is characterized by large areas of tall or mixed grass prairie with scrub oak forests on certain highland areas. These oak forests are quite xeric. Mesic forests of oaks and other hardwoods are found in stream floodplains and in deep ravines. All the Payne County collections were from Mesic forests. The McCurtain County sites were also Mesic in condition."

RELATIONSHIPS. M. R. Smith (1962) noted the apparent relationship between *exotica* and the Indo-Australian *Ponera* species. He concluded that *exotica* was probably introduced into the United States by man. These conclusions were based on his own studies, and on opinions ventured by the author (pers. comm.). I still subscribe to these views, though it would be desirable to see larvae of *exotica*. If they have 4 pairs of dorsal abdominal glutinous tubercles, as in *pennsylvanica*, I would assume them to be descended from the *coarctata* group. If this is so, the resemblance between *exotica* and *leae* would represent an almost unbelievable case of convergent evolution.

Exotica and *leae* are very similar, indeed, I have considered the possibility that they are merely races of a single species. I feel, however, that their separate status is justified, while admitting that a fully objective decision will depend on study of further material, especially larvae and males.

I suggest that *exotica* will eventually be found in the Papuasian area, and that *leae* represents a closely related Australian endemic species, derived from Papuasian stock.

Ponera tenuis Group

The following 4 species are characterized by possession of a 4-segmented antennal club in the female castes, and lack of an incised dorsal mesometanotal suture in the workers.

They superficially resemble the *leae* group, and the smaller members of the *japonica* group (*incerta* and *swezeyi*), being small light-brown species with worker head width ranging 0.30-0.45 mm.

The group is New Guinea based, with one species, *tenuis*, ranging eastward to Samoa. *Tenuis* is distinguished by relatively large size from the remaining species (*petila*, *szaboi*, and *szentivanyi*), which form a closely related series (referred to here as the *szentivanyi* complex).

Sexuals are known only for *tenuis*. They are normal for the genus, with wing venation of the "coarctata type." Larvae of *tenuis* have 3 pairs of dorsal abdominal "doorknob" tubercles, as usual in Indo-Australian species. Its pupae are unusual, in that they lack cocoons, a character differentiating them from all other species of the genus for which this stage is known. Pupae of the *szentivanyi* complex are not known. If they lack cocoons my worker-based species-group classification of the smaller *Ponera* species would gain support.

The species of the *szentivanyi* complex were all described by Wilson (1957). They are known only from the types; so my discussion of them essentially paraphrases that of Wilson, with a few supplementary descriptive notes. I am dubious about the status of these species. *Szaboi* could be an ecological variant of *tenuis*, especially considering the variability seen in *P. leae* around Sydney (see above). *Szentivanyi* is probably based on small nanitics of *tenuis*. The dimensions of the two known specimens appear to set them apart, but their apparent distinctiveness could be due to aberration caused by shrinkage, since both are callow. Increase of only 0.02 mm in the head width measurements of these specimens would bring their divergent cephalic and scape indices within the ranges of the *tenuis* material. *Petila*, on the other hand, seems to represent a good species.

26. *Ponera tenuis* (Emery) Figs. 83-85.

Cryptopone tenuis Emery, 1900, Természetr. Fü. 23: 321-322, pl. 8, figs. 21, 22, worker. Original localities: Lemien, near Berlinhafen (=Aitape,) and Tamara I., NE New Guinea.

Pseudocryptopone tenuis: Wheeler, 1933, Amer. Mus. Nov. 672: 13-14.

Ponera tenuis: Wilson, 1957, Bull. Mus. Comp. Zool., Harv. 116 (6): 373, fig. 2. Redescription of worker and queen from Ebabaang and Joangeng, NE New Guinea.

Ponera huonica Wilson, 1957, Bull. Mus. Comp. Zool., Harv. 116 (6): 365, fig. 2, worker, queen. Original locality: Ebabaang; additional localities: Gemeheng and Joangeng, NE New Guinea. (Holotype and Paratypes examined, MCZ.) **New Synonymy.**

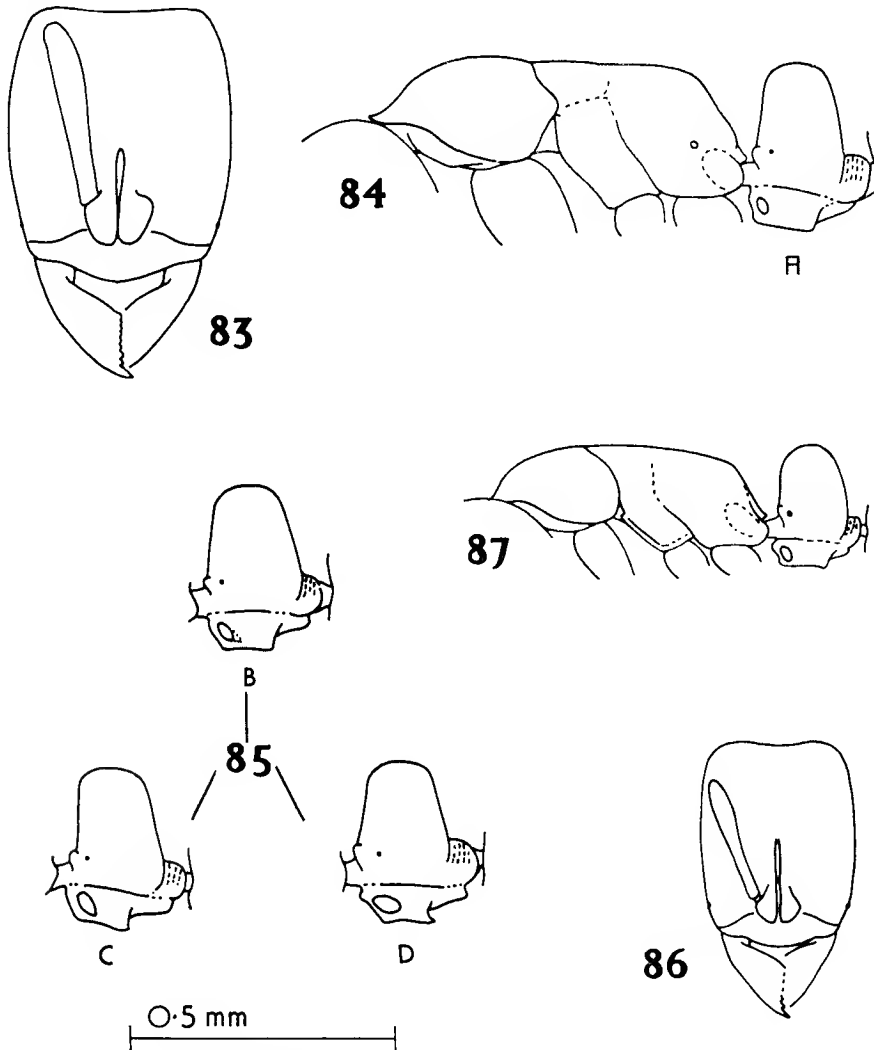
SYNONYMY. The synonymy of *huonica* under *tenuis* is based on examination of Wilson's specimens and study of additional material collected at Aiyura, New Guinea by me. The following features are significant:

1. Ranges for the standard measurements given by Wilson for the 2 species overlap broadly, with the exception of HW (cited as 0.40-0.41 mm for *huonica*, 0.42-0.44 mm for *tenuis*).

HW range in the Aiyura specimens exceeds these ranges together, and the same is true for most of their other dimensions (see Table 5).

2. The mandibular dentition of the *huonica* holotype is different from that of other small *Ponera* specimens. It appears, in the Wilson series, to characterize that species. The Aiyura material shows all intergrades between the extreme "*huonica* condition" (as described by Wilson 1957: 365) and the normal type. Moreover, the *huonica* paratypes do not show this character as strongly as the holotype.

3. The sub-petiolar process of the *huonica* holotype appears to be sharply truncated, as opposed to acutely dentate in *tenuis*. The condition here is, in fact, due to the presence



Figs. 83-87. Group of *Ponera tenuis*. *Ponera tenuis* (Emery) worker (Aiyura, New Guinea): 83, head; 84, mesosoma and node; 85, variation in petiolar node structure (for explanation see text). *Ponera szaboii* Wilson, worker (Holotype): 86, head; 87, mesosoma and node.

of a minute and deceptive fragment of mounting glue lying along the lower edge of the process. This character is, of course, not present in the *huonica* paratypes.

4. Variation in shape of the dorsal petiolar surface in the Aiyura specimens completely embraces the extremes for the two species as recognized by Wilson.

DIAGNOSIS. A widespread species known from E. New Guinea and Samoa. Its presence on intermediate island groups (especially the Solomons and Fiji) is likely.

Easily recognized by the combination of medium size (HW 0.40–0.45 mm) with the characters of its species group (4-segmented antennal club and lack of an incised mesometanotal suture). The other 3 *tenuis* group "species", with which *tenuis* is probably sympatric on New Guinea, are all smaller (HW 0.30–0.34 mm). In Samoa the species group characters are diagnostic. The absence of pupal cocoons provides a useful character for field recognition; this is the only known *Ponera* with naked pupae.

Additional description.

Worker: Dimensions of specimens used in this study are given in Table 5.

Wilson's (1957) redescription of a *tenuis* syntype, and his original description "*huonica*" cover general characters, but the following additional notes are pertinent:

1. Mandibular dentition varies intranidally in New Guinea samples. As usual in the genus, one observes 3 large apical teeth, followed by a series of 6–10 small denticles. In most specimens several denticles are larger than the others (usually one or 2 at about the middle of the series, and the posterior one). Minimally they are barely enlarged; maximally they are as large as the middle, or smallest, of the anterior trio of teeth. Only 2 of 30 New Guinean specimens have completely uniform denticle series. A regular row of denticles is usual in Samoan specimens, which show little tendency towards denticular heterogeneity.

2. Palpal formula: *Maxillary 2; Labial 2* (3 workers each from Aiyura and Samoa dissected).

3. Dorsal mesometanotal suture totally lacking in all specimens. It is sometimes represented by a narrow, but obtuse, impression, which never breaks the underlying sculpturation.

4. Structure of the subpetiolar process shows intrademe variation as illustrated in figs. 84 and 85 (variant types labelled A–D). The varying features include depth of the process, shape of its anterior and ventral outlines, size and shape of the fenestra, and degree of development of the posteroventral teeth. There is apparent geographical variation in expression of these characters. The samples differ as follows: Huon Peninsula specimens (including the "*huonica*" types) range in structure from type A (fig. 84) to type B (fig. 85), most being about intermediate. The Aiyura specimens range from type B to type C (fig. 85), most being about intermediate. The Samoan specimens are even less conservative, most have structure intermediate between types C and D (fig. 85—type D is a selected maximally bizarre example). At the other extreme a few Samoan specimens have type B petioles.

♀. Apart from slight quantitative differences ♀♀ show little variation. Wilson's 5 specimens, plus 6 from Samoa have the following dimensions: HL 0.51–0.59 mm; HW 0.43–0.51 mm; SL 0.35–0.42 mm; CI 80–86; SI 78–83; PW 0.29–0.33 mm; PNL 0.18–0.21 mm;

Table 5. *Ponera tenuis*: Dimensions of workers from the major study samples.

Sample	Wilson 1957 <i>tenuis</i> specimens	" <i>huonica</i> :" type series	Aiyura Material	Samoan Material	Total Ranges
Number of specimens	4	6	22	16	48
HL	49-52	48-50	48-53	48-52	48-53
HW	42-44	40-41	40-45	39-44	39-45
SL	33-35	33-35	33-36	32-35	32-36
CI	82-86	80-84	82-87	82-86	80-87
SI	78-83	81-87	77-85	78-87	77-87
PW	32 ¹	29-32	30-34	29-33	29-34
PNL	17	18 ²	19-21	17-20	17-21
PH	32	33 ²	30-32	30-33	30-33
DPW	22	22 ²	20-22	19-22	19-22
PNI	69		65-72	66-71	65-72

¹ lectotype only² holotype only

PH 0.32-0.36 mm; DPW 0.22-0.28 mm; PNI 68-74; maximum length of compound eye 0.28-0.30 mm; ocular index 31-37; palpal formula: *Maxillary* 2: *Labial* 2 (2 specimens dissected). Agreeing with the standard plan for the genus; diagnosed by size and the 4-segmented antennal club. Wing venation of "*coarctata* type."

♂. A single ♂ (*huonica* type series), described by Wilson (1957) is typical for the genus.

Immature stages: Larvae have 3 pairs of glutinous abdominal tubercles. Pupae of all castes lack cocoons (I have seen sufficient material to be sure that these are never spun).

DISTRIBUTION AND MATERIAL EXAMINED. All specimens listed here were studied, except the *tenuis* types. **NE NEW GUINEA**: Lemien near Berlinhafen (=Aitape); Tamara I. (Emery 1900) (Original Localities). *Huon Peninsula*: Mongi River water shed (E. O. Wilson), IV-1955; Ebabaang, 1300-1400 m [Wilson accs, 826 (3 workers), 827 (2 workers, 2 ♀♀, 1 ♂), 828 (3 workers)]; specimens from accs. 826 and 827 labelled as types of "*huonica*." The acc. 828 specimens were determined by Wilson as *tenuis*, by comparison with a syntype (Emery coll.). Gemeheng, 1300-1500 m [Wilson acc. 791 (worker and 2 ♀♀) — "*huonica*" paratypes]; Joangeng, near Ebabaang, 1500 m, [Wilson acc. 746 (dealate ♀) — "*huonica*" paratype]. *Eastern Highlands Distr.*: Aiyura, 1900-2000 m, rain forest, VI.1962 [R. W. Taylor accs. 2070, ex "zoraptera stage" rotting log (6 workers); 2076 ex rotting log (2 workers); 2139, worker ex berlesate; 2168, colony ex "zoraptera stage" rotting log (22 workers, 1 ♀)]. **SAMOAN IS.**: (R. W. Taylor and G. Ettershank are referred to by initials, accession numbers refer to MCZ material). In all, about 90 workers and ♀♀ have been examined. *Savaii*: Falealupo, nest ex rotten log, rain forest, 20.III.1962 (RWT acc. 435). Gagaifomauga, ground berlesates, 14.VI.1962 (GE accs. SI-S3). Matega, 70 m, strays under moss and leafmold on large boulders, banana clearing in rain forest, 20.III.1962 (RWT accs. 390, 391). Mt Matafa, 700 m, tree moss berlesate, 24.III.1962 (RWT acc. 588). Mt Olomanu, nest ex dead epiphyte, berlesates of moss on trees, moss and old

epiphytes on log, rain forest, 15.VI.1962 (GE accs. S7, S8, S10). *Upolu*: Afiamalu, 700 m, under moss on log, disturbed rain forest, 30.III.1962 (RWT acc. 632); berlesates, moss ex ground and rotting logs, disturbed rain forest, III-IV.1962 (RWT acc. 2321; GE acc. 53); tree moss berlesates, disturbed rain forest, III-IV.1962 [RWT accs. 580, 583, 2305, 2306, 2312 (all at 8-10 above ground; RWT acc. 581 (12 m above ground); GE acc. 45 (8-10 m above ground)]. Le Mafa, ground berlesates, rain forest, 13.V.1962 (GE accs. 62-64). Malololelei, 650 m, ground berlesate, 19.I.1956 (TEW). Tanumalala ground berlesate, 2.II.1956 (TEW). Tiapapata, berlesates, moss and epiphytes ex trees, 19.V.1962 (GE accs. 72, 74).

ECOLOGY. See above under *P. incerta*, where discussion of the comparative ecology of that species and *tenuis* is presented.

RELATIONSHIPS. See under species group heading.

27. *Ponera petila* Wilson

Ponera petila Wilson, 1957, Bull. Mus. Comp. Zool. **116** (6): 368, fig. 2, worker. Type locality: lower Busu River, Huon Peninsula, NE New Guinea (Holotype examined, MCZ coll.).

DIAGNOSIS. The species group characters (4-segmented antennal club, absence of an incised mesometanotal suture), and the small size, allow preliminary diagnosis. *Petila* may be separated from *szaboi* and *szeztivanyi* by the following characters:

1. From the probably sympatric *szaboi*, by slightly larger size (HW 0.32 mm, DPW 0.18 mm, opposed to 0.30-0.31 mm, and 0.15 mm respectively in *szaboi*). Proportionately longer scapes (SI 88; in *szaboi* 78-83), and broader petiolar node (PNI 72 against 65 in *szaboi*). Sculpturation of *petila* is considerably less intense than that of *szaboi* (compare the description below and that given under *szaboi*).

2. From *szeztivanyi*, by smaller size (HW 0.34 mm in *szeztivanyi*), broader head (CI 78, opposed to 75 in *szeztivanyi*), and other dimensional differences (*e. g.*, SI 88 in *petila*, 94 in *szeztivanyi*, etc.). Sculpturation of the head and mesosoma of *szeztivanyi* is about intermediate between that described for *petila* and that of *szaboi* discussed below.

Additional description. Wilson's description did not mention lack of an incised mesometanotal suture in the workers, or that the palpal formula appears to be *Maxillary* 2: *Labial* 2 (the mouthparts are only partially exposed; so a positive count is impossible).

Sculptural details required for diagnosis are: head moderately shining, with small point punctures separated by distances about equal to their maximum diameter. Pronotal dorsum fairly strongly shining, with scattered minute punctures; mesonotum almost imperceptibly more closely punctate. Lateral surfaces of mesosoma feebly shagreened to smooth and shining.

Wilson's dimensions of the holotype are: HW 0.32 mm; HL 0.41 mm; SL 0.28 mm; CI 78; SI 88; PW 0.25 mm; PNL 0.13 mm; PH 0.25 mm; DPW 0.18 mm; PNI 72.

♀, ♂ and immature stages unknown.

DISTRIBUTION AND MATERIAL EXAMINED. Known only from holotype worker. NE NEW GUINEA: lower Busu River near Lae, 10.V.1955 (Wilson acc. 999) MCZ. Collected in soil under a rotting log, in primary lowland forest.

This species is probably sympatric with *P. szaboi*, judging from Wilson's field data.

RELATIONSHIPS. See above under species group diagnosis.

28. *Ponera szaboi* Wilson Figs. 86-87.

Ponera szaboi Wilson, 1957, Bull. Mus. Comp. Zool. **116** (6): 371-372, worker. *Nom. Pro.* *Cryptopone mocsáryi* Szabó, 1910, Rovartani Lapok 17: 186 (*nec Ponera mocsáryi* Emery, 1900). Type locality: Friedrich-Wilhelmshafen (=Madang) NE New Guinea.

Pseudocryptopone mocsáryi: Wheeler, 1933, Amer. Mus. Novitates **672**: 14.

DIAGNOSIS. Known only from workers taken in coastal rain forest at several NE New Guinea localities. Preliminarily diagnosed by small size, with the *tenuis* group characters (4-segmented antennal club, lack of a differentiated mesometanotal suture). Distinguished from *petila* by characters given in the diagnosis of that species. Differing from *szentivanyi* as follows:

1. Size smaller (HW 0.30-0.31 mm, PW 0.23 mm, DPW 0.15 mm; opposed to 0.34 mm, 0.28 mm and 0.21-0.24 mm respectively in *szentivanyi*).

2. Scapes relatively short (SI 79-83, against 94 in *szentivanyi*).

3. Sculpturation of mesosoma less intense. In *petila* its lateral surfaces are very feebly shagreened, to smooth and shining; in *szentivanyi* they are moderately shagreened and opaque.

Additional description. The original description did not mention absence of an incised mesometanotal suture. Palpal formula: *Maxillary* 2; *Labial* 2 (by inspection). Diagnostically important sculptural characters thus: head subopaque, closely punctate, punctures coarser and more closely packed than in *petila*. Mesosomal dorsum moderately shining, closely and finely punctate (much as on frons of *petila*), mesonotal and propodeal dorsa distinctly more coarsely and closely punctate than pronotum. Dimensions of Wilson's (1957) specimens are: HW 0.30-0.31 mm; HL 0.40; SL 0.25 mm; CI 76-78; SI 79-83; PW 0.23 mm; PNL 0.15 mm; PH 0.24 mm; DPW 0.15 mm; PNI 65.

♀, ♂, and immature stages unknown.

DISTRIBUTION AND MATERIAL EXAMINED. NE NEW GUINEA: Friedrich-Wilhelmshafen (=Madang) (Szabó). Lower Busu River, near Lae, 2 workers (Wilson accs. 963, 1024) MCZ. Taken as strays on the floor of primary lowland rain forest. I have seen only the specimens used by Wilson, these agree with Szabó's description of the holotype, which was not available for study.

RELATIONSHIPS. Close to *petila*, with which it is apparently sympatric, and to *szentivanyi*.

29. *Ponera szentivanyi* Wilson

Ponera szentivanyi Wilson, 1957, Bull. Mus. Comp. Zool. **116** (6): 372-373, figs. 1, 2, worker.

Type locality: Karema, Brown River, Papua. (Holotype examined, MCZ coll.)

DIAGNOSIS. Known only from SE New Guinea. The 4-segmented club and lack of an incised mesometanotal suture allow placement to the *tenuis* group. Distinguished from *petila* and *szaboi* by characters given under their diagnoses.

Additional description. Mesometanotal suture lacking on mesosomal dorsum. Palpal for-

mula: *Maxillary* 2: *Labial* 2 (paratype inspected). Dimensions of holotype (listed first) and the single paratype are: HW 0.34 mm; HL 0.45 mm; SL 0.32 mm; CI 75; SI 94; PW 0.28 mm; PNL 0.16 mm; PH 0.29 mm; DPW 0.24 mm, 0.21 mm; PNI 86, 75.

♀, ♂, and immature stages unknown.

DISTRIBUTION AND MATERIAL EXAMINED. SE NEW GUINEA: Karema, Brown River, near Port Moresby, holotype and paratype (Wilson acc. 563) MCZ. Collected on the floor of primary lowland rain forest.

RELATIONSHIPS. *Szentivanyi* is apparently close to *petila* and *szaboi*. This species is possibly based on partially shrunken nanitics of *tenuis* (see above under species group diagnosis).

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